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Phylogeny of *Panthera*, Including *P. atrox*, Based on Cranialmandibular Characters

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A thesis  
presented to  
the faculty of the Department of Geosciences  
East Tennessee State University

In partial fulfillment  
of the requirements for the degree  
Master of Science in Geology

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by  
Leigha King  
May 2012

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Steven C. Wallace, Chair  
Blaine W. Schubert  
Jim I. Mead

Keywords: auditory bullae, cranial, dentary, morphology, *Panthera*, *P. atrox*, phylogeny

## ABSTRACT

Phylogeny of *Panthera*, including *P. atrox*, based on cranialmandibular characters

by

Leigha King

Over the past 20 years both morphological and molecular phylogenies have been proposed for extant and extinct members of the family Felidae. However, there remain several discrepancies, particularly within the genus *Panthera* and the position of *Panthera atrox*. Consequently, morphologic characters from the skull and dentary were analyzed within *Panthera* (including all extant and one extinct taxa) to gain a better understanding of pantherine phylogeny. Multiple specimens of each taxon were analyzed, including: *P. leo*, *P. tigris*, *P. onca*, *P. pardus*, *Uncia uncia*, and *Neofelis nebulosa*. Four outgroups were used; *Crocota crocuta*, *Metailurus* ssp., *Proailurus lemanensis*, and *Pseudaelurus validus*. From each phylogeny created, despite the outgroup, apparent grouping between *Panthera leo*, *P. tigris*, and *P. atrox* was present. Therefore, *P. atrox* is likely more closely related to the African lion and the tiger than the jaguar, in contrast to what has been recently suggested.

## DEDICATION

I would like to dedicate this study and the work within to my friends and family. Their support and constant interest in my research kept me excited about the project at hand. Many nightly conversations occurred regarding methods, conclusions, and other analyses that always kept me thinking and striving to complete the best research I could. Thank you!

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## CHAPTER 1

### INTRODUCTION

#### Research question

To date, several studies have attempted to better resolve the phylogenetic relationship of *Panthera atrox* to modern felids. However, very few reach the same conclusion, and even the relationships among modern pantherine cats are not completely understood. These inconsistencies suggest further analysis and perhaps even different methodology are required to better understand pantherine evolution. Here, the morphology of the mandible and cranium in extant *Panthera* was analyzed to gain a more complete understanding of its phylogeny as well as two related species, *Neofelis nebulosa* and *Uncia uncia*, that are commonly grouped within (or near) pantherines. Specifically, craniodental characters/ character suites for each species were analyzed to gain a better understanding of the phylogeny within the group and to elucidate the positioning of *P. atrox* within *Panthera*. Four different outgroups were used to interpret consistent relationships because the chosen outgroup often influences the phylogeny created.

#### Life history of modern pantherines

*Panthera* is debated to have originated in Asia between 3.8-10.8 Ma (Johnson et al. 2006; Davis et al. 2010). The genus often consists of four modern species, *P. leo* (African lion), *P. tigris* (tiger), *P. onca* (jaguar), and *P. pardus* (leopard). Each of these cats has been placed within the genus due to the presence of a ligament within the hyoid apparatus that enables roaring (Pocock 1916). Most also exhibit sexual dimorphism, with males growing much larger than females. Occasionally a fifth species, the snow leopard, *Uncia uncia*, is grouped within the genus depending on the phylogeny in question (Collier and O'Brien 1985). For the purpose of this

study *U. uncia* will not be included in the genus *Panthera* but will be included in the analyses. Though not a member of *Panthera*, the clouded leopard, *Neofelis nebulosa*, is also often grouped with the genus; together, including *U. uncia*, making up a larger group called pantherines (Johnson and O'Brien 1997).

*Panthera leo* can currently be found in parts of Africa and a small region in India (Figure 1) (Haas et al. 2005). However, the historic distribution also included regions near the Arabian Peninsula and Asia Minor (Guggisberg 1975). Seven extant and several extinct subspecies have been identified, including an extinct smaller Asian form (Mazak 2010). The oldest *P. leo* fossil was recovered in Tanzania and has been dated to around 3.5 Ma (Turner and Anton 1997; Haas et al. 2005). By the late Pleistocene, lions were present in most of Eurasia and North America (Figure 2)(Haas et al. 2005). Fossils from these regions have often been identified as *P. leo atrox* or *P. leo spelaea* leaving much controversy over whether some fossil specimens should be identified as subspecies of lion or separate species (Haas et al. 2005). Extant lions are social and will hunt in prides consisting predominantly of females and a few dominant males. Prey typically includes wildebeest, zebra, buffalo, giraffe, and warthog; however, they will also readily scavenge (Guggisberg 1975; Alderton 1993; Turner and Anton 1997; Haas et al. 2005).

*Panthera tigris* is the largest living felid and is currently found in remote populations in India, Nepal, Malaya, China, Siberia, and Sumatra (Figure 1) (Guggisberg 1975; Mazak 1981; Alderton 1993; Turner and Anton 1997). From these populations, eight subspecies have been identified (Guggisberg 1975). Before human interaction, tigers were found from the Caspian Sea to Indian, across Southeast Asia into China (Guggisberg 1975; Mazak 1981; Alderton 1993; Turner and Anton 1997). It is believed that extinct forms of tiger likely occupied the same range as the modern species (Turner and Anton 1997). Recently, several fossils from the early

Pleistocene have been recovered in China that suggest ancestors to the tiger lineage occurred as early as 2.55-2.16 Ma (Figure 2) (Mazak et al. 2011). Extant tigers are solitary, with the exception of a female with cubs (Mazak 1981; Nowak 1999). Hunting usually occurs at night and typical prey items include bear, deer, pig, gaur (Indian bison), monkeys, Siberian moose, and Indian buffalo (Mazak 1981; Turner and Anton 1997; Nowak 1999).

*Panthera onca* is one of the smaller living species within the genus (though the species was much larger in the past (Seymour 1989; Seymour 1993)). Modern jaguars are found only in Central and South America (Figure 1) (Guggisberg 1975; Alderton 1993). However, Pleistocene records and personal accounts prior to the 1900s indicate the jaguar was present in North America and has been found in California, Arizona, Texas, Nebraska, Louisiana, Arkansas, Tennessee, Florida, West Virginia, and Pennsylvania (Figure 2) (Guggisberg 1975; Corgan 1976; Alderton 1993; Seymour 1993; Turner and Anton 1997; Nowak 1999; Seymour 2003; Schubert personal communication;). Recent reports suggest a small population has begun to develop in southern Arizona and New Mexico (McCain and Childs 2008). An extinct subspecies, *P. onca gombaszoegensis*, has also been reported from the Pleistocene of Europe (Hemmer et al. 2001). The oldest *P. onca* remains in North America are dated to 820-850 ka (Middle-to-late Irvingtonian) (Kurten and Anderson 1980; Seymour 1989; Seymour 1993). Jaguars vary in size depending on their geographic location or altitude, with smaller individuals present near the equator and larger members near the northern and southern limits of the species' range or at higher elevations (Seymour 1989). Size has also decreased over time as indicated by Pleistocene specimens having much longer limbs and metapodials than their modern counterparts (Seymour 1989; Seymour 1993; Turner and Anton 1997).

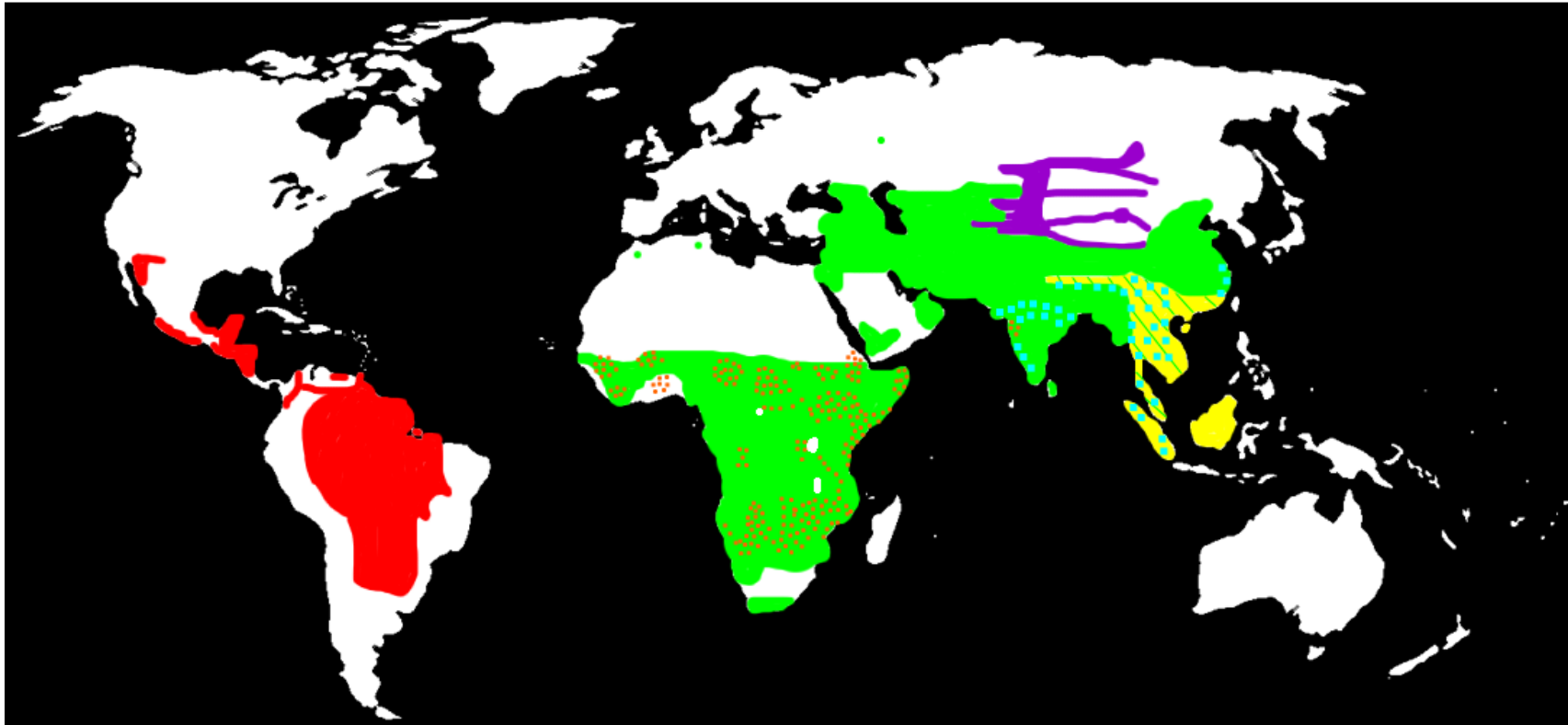


Figure 1. Distribution of modern pantherine species modified from Hemmer (1972), Guggisberg (1975), Mazak (1981), Alderton (1993), Turner and Anton (1997), Haas et al. (2005), Nowak (2005), and McCain and Childs (2008). Each color represents a different species and where overlapping ranges occur, the species is represented by stripes or dots; *Neofelis nebulosa* yellow, *Uncia uncia* purple, *Panthera pardus* green, *P. onca* red, *P. tigris* blue dots, *P. leo* orange dots.

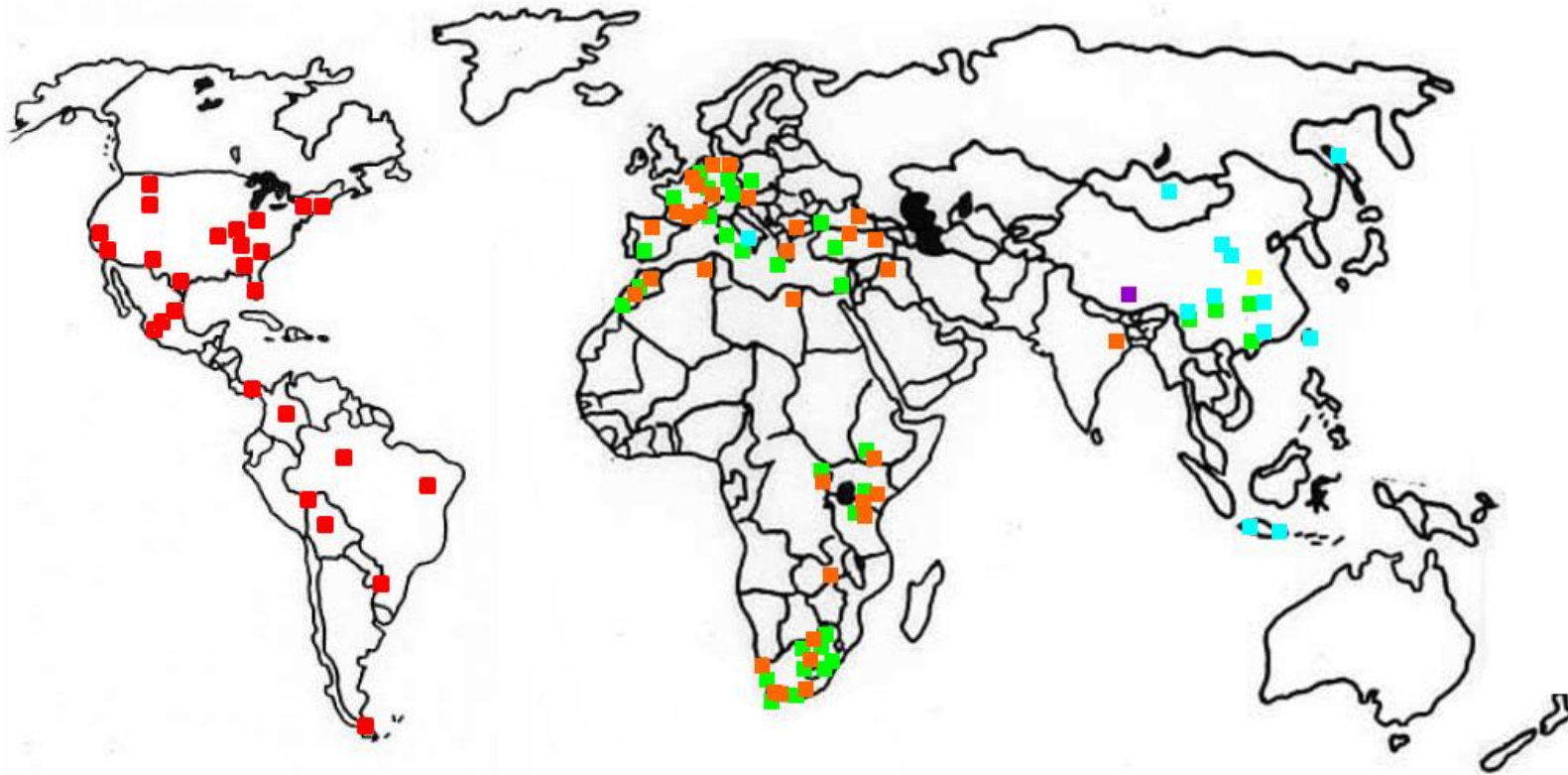


Figure 2. Fossil localities (Pleistocene) of extant pantherine genera modified from Hemmer (1972), Guggisberg (1975), Mazak (1981), Seymour (1993), Turner and Anton (1997), Seymour (2003), Haas et al. (2005), Liu et al. (2009), and Schubert, personal communication. Each color represents a different species, while each point represents a different fossil locality; *Neofelis nebulosa* yellow, *Uncia uncia* purple, *Panthera pardus* green, *P. onca* red, *P. tigris* blue, *P. leo* orange.

As with many other species in *Panthera*, the jaguar is solitary and preys on mammals such as capybara, tapir, deer, armadillo, and peccary (Guggisberg 1975; Seymour 1989). These cats are also adept swimmers and have been known to hunt fish, turtles, and small alligators (Guggisberg 1975).

*Panthera pardus* is currently found in Africa, the Middle East, Asia, and the Malaysian archipelago (Figure 1) (Alderton 1993). Historically, the distribution of the leopard was much greater and also included regions around the Cape of Good Hope to the Mediterranean Sea (Guggisberg 1975; Alderton 1993; Turner and Anton 1997); with fossils of *P. pardus* occurring from the Pleistocene of Europe and Africa (0.9Ma) (Figure 2) (Turner and Anton 1997). Like most of the species within *Panthera*, the leopard is solitary and occupies a diverse range of habitats (Guggisberg 1975). The main prey of *P. pardus* include gazelle, impala, baboon, porcupine, deer, jackal, stork, and goats (Guggisberg 1975; Turner and Anton 1997; Nowak 1999).

*Neofelis nebulosa* is characterized among the pantherine cats by its diagnostically long upper canines (Nowak 2005). Currently, *Neofelis* occupies forests in Nepal, Sikkim, Bhutan, Myanmar, Malaya, Siam, Indochina, S. China, Hainan, Borneo, Sumatra, Fukien, and Formosa (Figure 1) (Guggisberg 1975; Alderton 1993). It has been recently proposed that two species within *Neofelis* exist, *N. nebulosa* and *N. diardi* (Kitchener et al. 2006). The species has been identified from the Pleistocene of China (Figure 2) (Liu et al. 2009). The clouded leopard was previously thought to be a highly arboreal species; however, more recent studies have shown that this cat is predominantly terrestrial (Guggisberg 1975). Prey includes birds, monkeys, pigs, cattle, goats, and deer (Nowak 2005).

*Uncia uncia*, is found in mountain ranges in the Middle East and Asia (Figure 1) (Hemmer 1972; Guggisberg 1975; Alderton 1993; Turner and Anton 1997; Nowak 2005). The fossil record for this species is scarce, and many specimens originally identified in the 1800s are likely a misidentification (Hemmer 1972; Turner and Anton 1997). However, recent finds on the Tibetan Plateau suggest the ancestors to the species were present during the Pliocene (Figure 2) (Wang personal communication). Little is known about the social structure of the snow leopard, but individuals tend to be isolated in the wild (Hemmer 1972). Prey include blue sheep, goat, ibex, bharal, marmot, boar, deer, and pika (Hemmer 1972; Guggisberg 1975; Turner and Anton 1997; Nowak 2005).

#### History of *Panthera atrox*

Leidy (1853) first named *Felis atrox* from a portion of mandible found in Natchez, Mississippi. He noted its affinities to the modern lion, “*Felis*” *leo*, and thus designated it the American lion. Merriam and Stock (1932) described in detail the specimens of *F. atrox* from the tar pits at Rancho La Brea (CA) and suggested the skulls of the extinct cat shared characteristics with both lions and tigers but lacked many similarities with jaguars. The species was later assigned to *Panthera* by Simpson (1941) who also proposed the “lion” may in fact hold more affinities with jaguars. Kurten and Anderson (1980) renamed *P. atrox* as a subspecies of the modern lion; thus assigning the name *P. leo atrox*. Currently, both *P. atrox* and *P. leo atrox* can be seen in the literature depending on the authors’ opinions. However, still under discussion is the relationship among *P. atrox*, *P. leo*, and *P. onca* and whether the American lion should be considered a relative to the modern jaguar (Simpson 1941; Christiansen 2008A; Christiansen and Harris 2009). Wheeler and Jefferson (2009) suggest *P. atrox* was highly dimorphic, perhaps more so than the modern lion. Because *P. onca* does not exhibit dramatic dimorphism, it could

suggest a closer relationship between *P. atrox* and *P. leo* than with *P. onca* (Wheeler and Jefferson 2009; Meachen-Samuels and Binder 2010).

*Panthera atrox* is known from fossil localities spanning North America including California, Alaska, Wyoming, Colorado, Florida, Kansas, Missouri, Texas and Mexico to name a few (Kurten and Anderson 1980) (Figure 3). To date, a total of 110 specimens of *P. atrox* from the tar pits of Rancho La Brea have been catalogued, though some are isolated elements and teeth. Fossils of different species and artifacts within the various pits have been dated between 44,000 and 5,000 years old (Marcus and Berger 1984). Carnivorans constitute 91% of the fossils uncovered from Rancho La Brea (Marcus 1960), 40% of which are represented by cats (Stock 1929). Taphonomic studies of the site suggest carnivorans, such as *P. atrox*, were responsible for scattering and eliminating bones from prey such as bison (Stock 1929; Spencer et al. 2003). In addition to the attraction of struggling prey, scavenging could explain the high proportion of carnivorans trapped within the pit (Stock 1929; Spencer et al. 2003). Natural Trap Cave (WY) is another locality that has produced several individuals of *P. atrox* (Wang and Martin 1993). Animals passing the area would fall into the pit or become enticed by food and become trapped, resulting in death from injury (Wang and Martin 1993). To date, eight specimens have been collected (Wheeler and Jefferson 2009). Radiocarbon dates of the bones within the cave suggest an age range of 21,000-12,000 years old (Wang and Martin 1993). Wheeler and Jefferson (2009) have identified the specimens from Natural Trap Cave as predominantly female and suggested females were the more active hunters of the two sexes, as is true with modern lions. Other specimens of *P. atrox*, including a partial jaw and isolated canine, have been recovered in Chiapas, Mexico (Montellán-Ballesteros and Carbot-Chanona 2009). This locality has been described as Pleistocene in age based on the presence of *Glyptotherium* sp.



and *Equus conversidens* (Montellán-Ballesteros and Carbot-Chanona 2009). Several specimens of *P. atrox* have also been recovered in Alaska (Whitmore and Foster 1967). These specimens differ slightly in mandible shape from those described from Rancho La Brea (Simpson 1941; Whitmore and Foster 1967). This difference led Simpson (1941) to erect a distinct subspecies, *P. atrox alaskensis*. An additional specimen has been described from Florida and consists of a complete skull and dentary (Hulbert 2001).

*Panthera atrox* is found within the Rancholabrean North American Land Mammal Age (NALMA), which is defined by the presence of *Bison* south of 55°N latitude (Bell et al. 2004) or the immigration of the microtine rodents *Dicrostonyx* and *Lemmus* (Bell 2000). As is suggested by its name, the type locality for the Rancholabrean is the tar pits of Rancho La Brea in Los Angeles, California (Bell et al. 2004). Other taxa that represent this time include *Canis dirus*, *Megalonyx jeffersoni*, *Platygonus compressus*, and *Miracinonyx trumani* (though not extremely common) (Bell et al. 2004). The Rancholabrean occurs during the late Pleistocene and ends with the extinction of the megafauna (Bell 2000; Bell et al. 2004).

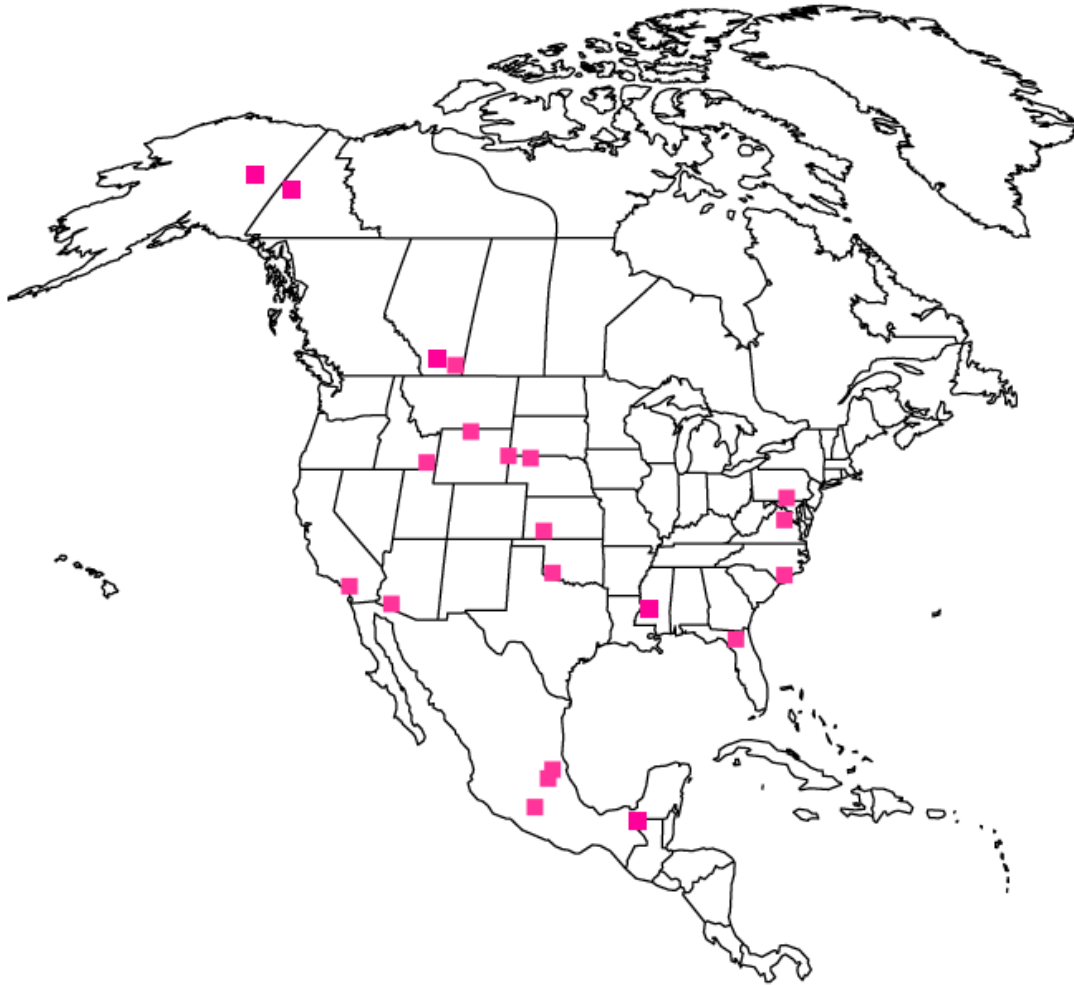


Figure 3. Distribution of fossil localities containing *Panthera atrox* modified from Whitmore and Foster (1967), Kurten and Anderson (1980), and Montellán-Ballesteros and Carbot-Chanona (2009). Each point represents an individual fossil local.

### History of outgroups

Four outgroups were chosen here: *Crocota crocuta* (spotted hyena), *Metailurus* ssp., *Proailurus lemanensis*, and *Pseudaelurus validus*. The spotted hyena was chosen based on the frequent use of Hyaenidae as an outgroup in phylogenetic studies on Felidae (e.g. Collier and O'Brien 1985; Johnson and O'Brien 1997; Holliday and Stepan 2004; Yu and Zhang 2005). While *C. crocuta* is a highly derived species, it was also chosen to determine whether similar trees would be produced when using morphological instead of molecular characters. *Metailurus* ssp., *Proailurus lemanensis*, and *Pseudaelurus validus* were all chosen due to their basal relationship within felids (Turner and Anton 1997). Because these species are thought to be basal felids, their traits should represent true ancestral states, making them ideal outgroups.

*Crocota crocuta* is found today mainly in sub-Saharan Africa and lives in large social groups called clans that typically have 50-90 members (Holekamp and Smale 1998; Holekamp et al. 2007). Clans will split and reform depending on resource availability (Holekamp et al. 1997). Within these clans, females are the dominant and more aggressive of the sexes (Holekamp and Smale 1998; Nowak 1999). A female will spend her entire life with her natal clan, while males leave upon reaching an age of 2-5 years (Holekamp et al. 1997; East and Hofer 2001). Immigrant males achieve a higher status by remaining in the same clan for a long period of time (East and Hofer 2001). The main prey of *C. crocuta* are medium sized ungulates such as wildebeest (Nowak 2005). Fossil specimens of *C. crocuta* have been recovered from the latest Pliocene-earliest Pleistocene in Kenya and South Africa (Ewer 1958). Fossils from both regions were dated to at least 1.8 Ma and also contained other fossils of artiodactyls, rodents, and primates (Ewer 1958; Harris et al. 1988). Several other Pleistocene localities have been identified from Africa, Europe, and China (Figure 4).

*Metailurus* consists of several species, including *M. major*, *M. minor*, *M. boodon*, and *M. parvulus* (Zdansky 1924; ; Belyaeva 1948; Tao et al. 2004; Anderson and Werdelin 2005) and is found worldwide, including Africa, Asia, Europe, and North America (Figure 4)( Zdansky 1924; Qiu 1989; Leakey and Harris 2003; Tao et al. 2004; Anderson and Werdelin 2005). *Metailurus major* was first described from Tai-Chia- Kou, China by Zdansky (1924); however, the age of this specimen is unclear. Other specimens of *Metailurus* from China have been found in the Liushu Formation (Tao et al. 2004). Specimens from this locality are late Miocene in age and include *Metailurus* sp. and *M. minor* (Tao et al, 2004). Pliocene remains of *Metailurus* sp. have also been recovered by Shanxi, China and date to 5.3-3.2 Ma (Qiu 1989; Anderson and Werdelin 2006). Specimens from Kenya also represent *Metailurus* sp. and are believed to be Miocene in age (11.6-7.2Ma) (Leakey and Harris 2003). The oldest remains in Europe date to approximately 8.0 Ma and have been found in Spain, Italy, Hungary, Ukraine, and Greece and represent *M. major* and *M. boodon* (Belyaeva 1948; Turner and Anton 1997 ; Roussiakis 2001). Middle Pleistocene specimens from Nebraska have tentatively been assigned either to *Metailurus* or *Pseudaelurus* (Barbour 1934). During the early Pliocene it is thought that all species of *Metailurus* went extinct (Turner and Anton 1997), suggesting the Nebraska specimens have been misidentified.

*Proailurus lemanensis* has often been referred to as the first true cat (Turner and Anton 1997). It was originally discovered in Quercy, France and consists of multiple mandibles and auditory regions (Turner and Anton 1997; Hunt 1998; Peigné 1999). Specimens from this locality, and an additional site in Mongolia, have been dated to around 30 Ma, or middle Oligocene in age (Sulimski 1970; Turner and Anton 1997; Hunt 1998). *Proailurus lemanensis* has also been recovered from a site in Germany and dated to approximately 21 Ma (Ziegler

1990). A similarly aged site in Spain (Daams 1974) has also produced a specimen of *Proailurus* sp. (Figure 4). While considered a true cat, *P. lemanensis* retains many primitive characters such as additional teeth and an elongate body (Turner and Anton 1997).

*Pseudaelurus validus* first occurs during the early Miocene (Stock 1934; Rothwell 2001; Holliday and Steppan 2004), about 20 Ma, and is believed to be ancestral to both modern felids and saber-toothed cats (Turner and Anton 1997). Multiple species exist within this genus, including *P. quadridentatis*, *P. transitorius*, and *P. lorteti* (Turner and Anton 1997).

*Pseudaelurus* is known from several localities worldwide that range in age from Miocene to Pleistocene (Figure 4) (Weiwen et al. 1995; Rothwell 2001; Tao et al. 2004). Most specimens are identified from mandibular and maxillary fragments (Rothwell 2001). Miocene localities containing the genus occur in China, Europe, and North America (Tao et al. 2004). *Pseudaelurus validus* was first described by Rothwell (2001) from the Española Basin of New Mexico and consisted of both cranial and postcranial material. Other fauna at the site age this specimen to late Hemingfordian (Miocene) (Rothwell 2001). The Pleistocene locality, from the Guizhou Province in Southern China, also contains specimens of *Panthera tigris* and *P. pardus* (Weiwen et al. 1995), so could be a misidentification.

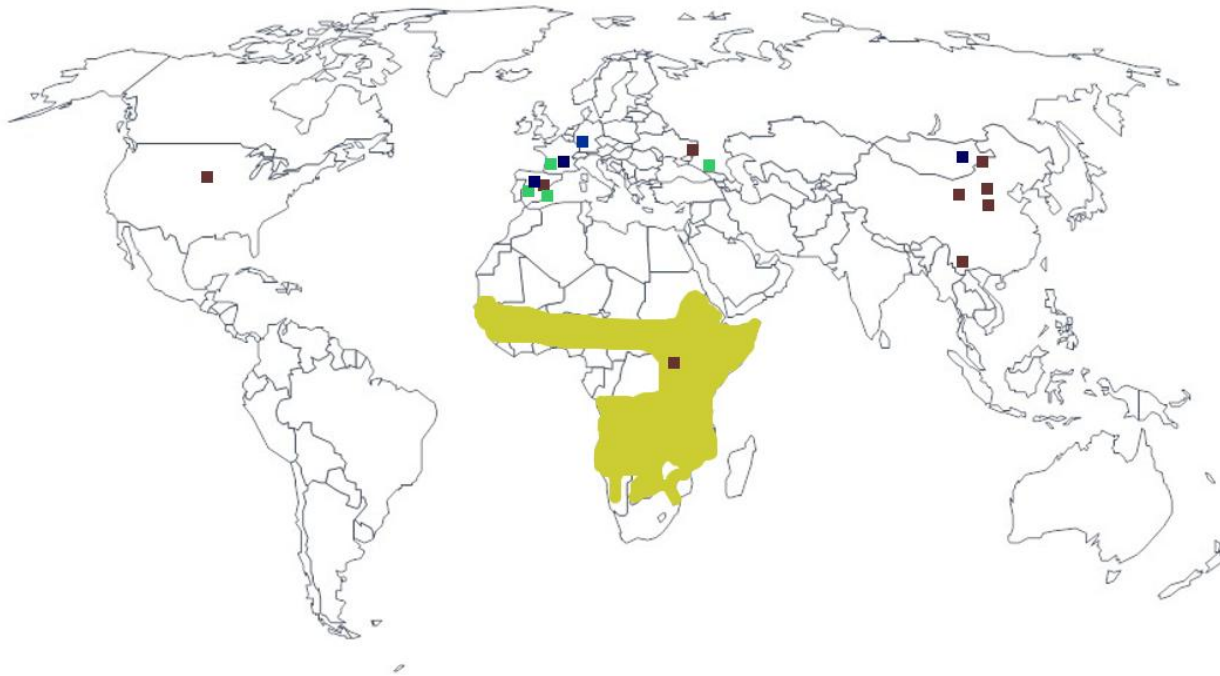


Figure 4. Distribution of modern and fossil localities of the outgroups used here modified from Zdansky (1924), Barbour (1934), Belyaeva (1948), Ewer (1958), Sulimski (1970), Daams (1974), Harris et al. (1988), Qui (1990), Zeigler (1990), Weiwen et al. (1995), Turner and Anton (1997), Hunt (1998), Peigné (1999), Rothwell (2001), Roussiakis (2001), Leakey and Harris (2003), Tao et al. (2004), and Anderson and Werdelin (2005). Each color represents a different species; *Crocuta crocuta* yellow, *Metailurus* ssp. brown, *Proailurus lemanensis* blue, *Pseudaelurus validus* green

### Previous phylogenies

Over the past 20 years both morphological and molecular phylogenies have been generated with the intent to better understand the evolutionary history of both extant and extinct members of the family Felidae (e.g., Johnson and O'Brien 1997; Yu and Zhang 2005; Christiansen 2008A; Barnett et al. 2009; Christiansen and Harris 2009; Davis et al. 2010). However, due to the very recent diversification within the family, there remain several discrepancies with both methods, particularly within the genus *Panthera*. Johnson and O'Brien (1997), for example, proposed that the extant Felidae consisted of three lineages including the ocelot, domestic, and pantherine lines. Pantherines were proposed to contain the puma, Asian leopard cat, caracal, and bay cat groups based on mitochondrial DNA (Johnson and O'Brien 1997). In addition, the phylogenetic trees suggested that the clouded and snow leopards are basal to the genus *Panthera* (Figure 5A). A similar conclusion was also made by Collier and O'Brien (1985); however, the Canadian lynx (*Lynx*) was placed closer to *Panthera* instead of the clouded leopard (Figure 5B). The snow leopard was not included in that study. A later study (Barnett et al. 2009), using mitochondrial DNA, analyzed *Panthera leo*, *P. "leo" spelaea* (cave lion), *P. "leo" atrox*, and *P. spelaea vereshchagini* (Beringian lion) to determine if the fossil species were truly a subspecies of the African lion, as had been previously proposed. Barnett et al. (2009) concluded that none of the fossil species were subspecies of the African lion, and more specifically, that *P. atrox* and *P. spelaea* are sister clades (Figure 5C). A similar conclusion was reached by Burger et al. (2004) in relation to *P. spelaea*. However, Yu and Zhang (2005) analyzed three phylogenetic trees created based on  $\beta$ -fibrinogen intron 7, and NADH dehydrogenase genes ND2 and ND4, and concluded within *Panthera* that the tiger is a sister

taxon to the rest of *Panthera* and that *U. uncia* and *P. pardus* are sister species. Samples for their study were taken from 14 felids, including every living representative of *Panthera* (Figure 5D) (Yu and Zhang 2005). More recently, Davis et al., (2010) concluded using Y-specific haplotypes that lions and leopards were monophyletic, with jaguars acting as a sister species. In addition, they concluded that tigers and snow leopards are sister species (Figure 5E).

As with molecular studies, there have been several morphological studies analyzing the phylogeny of Felidae. Salles (1992) conducted a phylogenetic analysis incorporating several species of Felidae using only cranial and dental characters. The phylogenetic tree produced from that study suggested *U. uncia* was basal to *N. nebulosa*, followed by *P. tigris*. The remaining species within *Panthera* were the most derived and all shared a single node (Figure 6A) (Salles 1992). Christiansen (2008A) looked at the pantherine cats, including six extant species (*N. nebulosa*, *U. uncia*, *P. tigris*, *P. onca*, *P. pardus*, and *P. leo*) and three fossil species (*P. palaeosinensis*, *P. spelaea*, and *P. atrox*). Based on 45 osteological, dental, soft tissue, and behavioral characters, Christiansen (2008A) concluded that *P. spelaea* and *P. atrox* were not lions. The study further suggested a paleo-jaguar lineage for *P. atrox* (Figure 6B). Christiansen and Harris (2009) conducted another study in which *P. atrox* was compared to the African lion, the tiger, and the jaguar using 36 linear and 6 angular measurements from skulls of each species. Both a warp and discriminant analyses were then assessed, from which Christiansen and Harris (2009) concluded that *P. atrox* was more jaguar than lion-like.



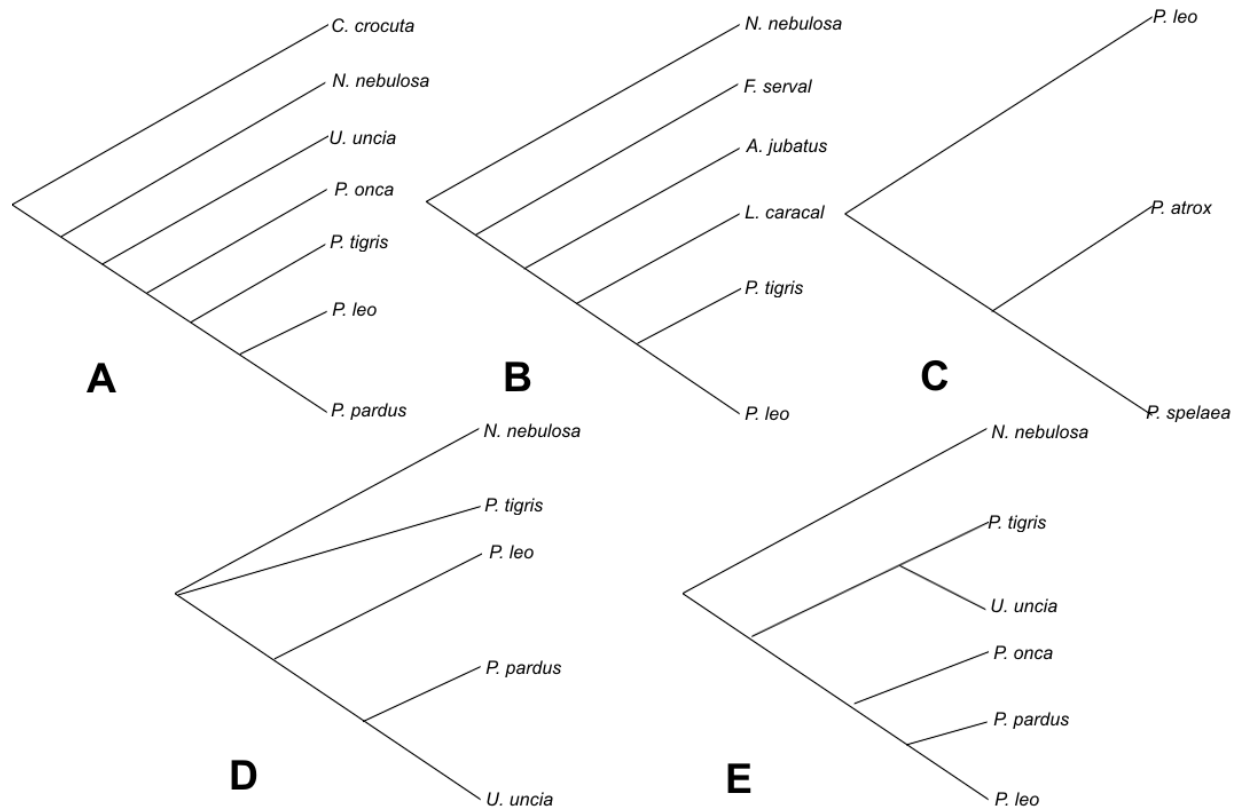


Figure 5. Molecular phylogenies of *Panthera* modified from A) Johnson and O'Brien 1997, B) Collier and O'Brien 1985, C) Barnett et al. 2009, D) Yu and Zhang 2005, E) Davis et al. 2010.

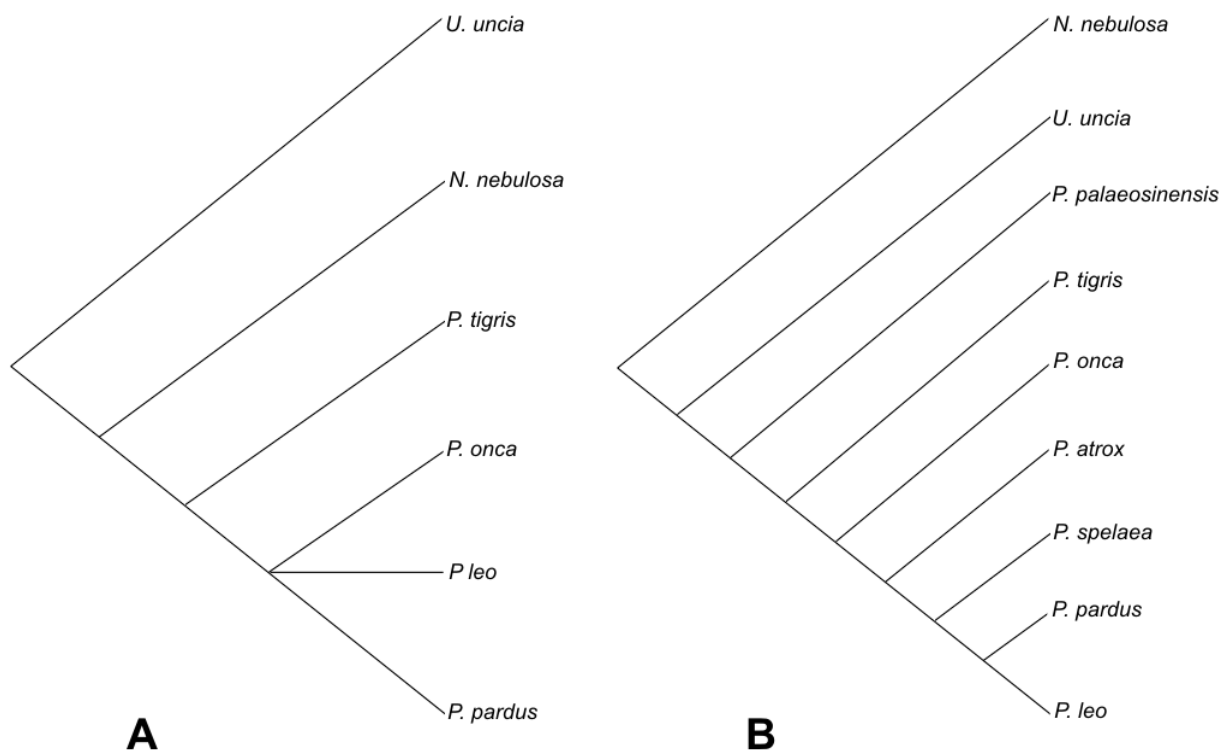


Figure 6. Previous morphological phylogenies of *Panthera* modified from A) Salles 1992, B) Christiansen 2008A.

## CHAPTER 2

### METHODS

#### Specimens analyzed

Specimens analyzed here are housed at the National Museum of Natural History (NMNH), American Museum of Natural History (AMNH), University of Florida (UF), and Natural History Museum of Los Angeles County (LACM). From these collections *C. crocuta* (n=25), *Panthera leo* (n=122), *P. tigris* (n=81), *P. pardus* (n=119), *N. nebulosa* (n=13), *U. uncia* (n=11), *P. atrox* (n=77), *Metailurus* ssp. (n=5), *Proailurus lemanensis* (n=1), and *Pseudaelurus validus* (n=3) were analyzed (Appendix I). Most of the *N. nebulosa* specimens lacked location data, and so it was assumed based on morphology that each individual was actually *N. nebulosa* (as their labels indicated) and not *N. diardii*. Zoo specimens were excluded from the study because they are subject to diseases and bone deformation, including arthritis, metabolic bone diseases, and dental caries, typically not seen in their wild counterparts (Glick et al. 1979; Caligiuri et al. 1989; Rothschild et al. 1998; Lynch et al. 2002). Mcphee (2004) and Howell (1925), for example, noticed changes in skull morphology due to captivity in both mice and male lions. Because skull morphology is vital here, using only wild specimens ensured that the true variety of traits commonly exhibited by a species was recorded.

### Statistical analyses

Several of the characters used here are measurements of either distance or angles between cranial structures. The measurements were obtained using the program Image J on photographs of each specimen. Measurements were taken on 20 different individuals of each species, with the exception of *U. uncia* and *N. nebulosa* due to 20 individuals not being available for analysis. Each available specimen of *P. atrox* was also measured, even if only a single measurement could be taken on a given specimen. Because measurements are not discrete characters, it was essential to find a means of defining character states. In order to do this, three different statistical analyses were used: principle component analysis (PCA), stepwise discriminant analysis (Stepwise DA), and histograms. All statistical analyses were conducted using SPSS for Windows (version 20.0; SPSS Inc., Chicago Illinois). Separate analyses were run for each outgroup that included all the species within the analysis. A total of 13 measurements were entered for *C. crocuta*, 12 for *Metailurus* ssp., 9 for *Proailurus lemanensis*, and 10 for *Pseudaelurus validus*. Differences in the number of measurements entered in each analysis was the result of preservation or cast quality. Table 1 lists the average measurement for each species for a given character.

The purpose of a PCA is to determine the variation between given specimens without assigning any preconceived groupings. See Dodson (1975) and Zelditch et al. (2004) for a detailed description on PCA. The original data matrix is projected into multidimensional space and from this projection variation is calculated and conveyed as principle components. The first component explains the greatest amount of variation within the data, the second component explains the second greatest amount of variation, and so forth. The Eigenvalues produced for each component represent the percentage of total variation within the data that a single component explains. In many cases, size accounts for the greatest variation between specimens

and is often the first principle component. For this reason, all length measurements were standardized by creating a ratio of the measurement to skull length. A PCA will remove a specimen from the analysis if data are missing for any one variable. To ensure that every specimen was still included, missing data were replaced with the average measurement value for that particular species. The goal for this analysis was to determine if the variables could separate each species from each other without any pre-assigned groupings present. A separate PCA was run for each outgroup, resulting in four different analyses.

Table 1. Averages for each linear measurement used within statistical analyses

Species	ABA	Par-Mast	m1	POA	Hypo	P4	I3/I2	C/c	C/sk	Hypo-Jug	PO-OA	FM	Par
Cc	36.71	0.05	2.45	75.78	0.02	3.47	1.70	0.97	0.13	27.52	92.61	0.12	0.30
Msp	37.62	0.06	4.16	95.33	0.47	3.17	1.94	x	0.12	35.81	96.51	0.19	0.24
Plem	26.47	0.75	2.65	101.22	0.21	2.71	x	0.91	x	x	88.26	x	x
Pv	25.01	0.08	2.36	97.10	0.41	3.13	x	x	x	31.44	x	0.09	0.14
Uu	37.24	0.04	2.09	97.64	0.02	2.92	1.51	1.29	0.16	35.73	94.07	0.21	0.16
Nn	32.43	0.05	2.21	79.97	0.02	2.99	1.57	1.31	0.23	39.10	93.96	0.16	0.23
Po	32.56	0.06	2.00	88.62	0.02	2.80	1.55	1.30	0.21	33.62	98.54	0.18	0.29
Pp	34.39	0.04	2.17	88.59	0.02	2.94	1.77	1.08	0.19	32.78	98.77	0.20	0.25
Pt	38.55	0.03	2.05	96.58	0.01	2.97	1.56	1.22	0.17	39.92	97.65	0.17	0.26
Pleo	37.71	0.02	1.91	97.89	0.01	2.73	1.56	1.25	0.15	31.59	92.22	0.16	0.23
Pa	31.76	0.05	1.93	100.63	0.02	2.74	1.80	0.96	0.16	39.55	97.08	0.22	0.28

Abbreviations are as follows: Cc *Crocota crocuta*, Msp *Metailurus* sp., Plem *Proailurus lemanensis*, Pv *Pseudaelurus validus*, Uu *Uncia uncia*, Nn *Neofelis nebulosa*, Po *Panthera onca*, Pp *Panthera pardus*, Pt *Panthera tigris*, Pleo *Panthera leo*, Pa *Panthera atrox*, ABA angle of auditory bulla, Par-Mast ratio of the distance between the mastoid process and paroccipital process to skull length, m1 ratio of m1 length to width, POA angle between postorbital process and posterior maxilla, Hypo ratio of the diameter of the hypoglossal foramen to skull length, P4 ratio of P4 length to width, I3/I2 ratio of length of I3 to I2, C/c ratio of length of upper canine to lower, C/sk ratio of upper canine length to skull length, Hypo-Jug angle between the hypoglossal and jugular foramina, PO-OA angle between the paroccipital process and occipital condyle, FM ratio of the distance from the postorbital process to the frontal maxillary suture divided by skull length, Par ratio of the distance from the postorbital process to the frontal parietal suture divided by skull length.

A stepwise DA attempts to find the most parsimonious way of distinguishing between assigned groups within the data. The assumption is made, therefore, by the analysis that there is in fact a correlation between variables and taxa. In addition, the importance of individual variables is assessed and those that have little effect on separating the assigned groups are removed from the analysis. See Zelditch et al. (2004) for a complete explanation of DA. Here, the assigned groups were each species of cat and the respective outgroup. A stepwise DA was chosen to determine which measured characters were statistically significant enough to separate each species. Those variables removed by the stepwise DA were not scored and were excluded from the phylogenetic analysis. As with the PCA, a separate stepwise DA was run for each outgroup.

Once a variable was determined to be significant by the stepwise DA, it was plotted on a histogram, where the variation within each species would be more apparent. From this histogram phylogenetic scores were assigned. This was done by dividing the histogram into sections based on the location of the outgroup. All species occupying the same morphospace as the outgroup were assigned a score of zero. Species occupying a portion of the morphospace containing the outgroup were typically assigned a score of one and all those species completely outside the outgroup morphospace were assigned a score of two (Figure 7) (Appendix VI).

### Phylogenetic analyses

It was important here to focus on those cranial characters that would be most closely tied to phylogeny instead of function (and thus similarities between species due to convergence). Therefore, the focus was the basiocranium and teeth, as seen in Wang and Tedford (1994) for canid phylogeny. Some of these characters included development of the metaconid on the lower

carnassial, number of cusps on the incisors, and the shape and development of the mandibular and paroccipital processes. Location and shape of various foramina were also analyzed. For example, the size and proximity of the foramina on the lacrimal was analyzed, as well as positioning of the foramen rotundum and foramen ovale on the skull. Unlike previous morphological studies, no soft tissue traits were used here as they cannot be scored for extinct taxa. See Appendixes II-V for a list of character descriptions for each outgroup. Characters were scored on all the specimens within the study, even if only partial skulls were available.

Four matrices were created for each distinct outgroup; *Crocota crocota*, *Metailurus* ssp., *Proailurus lemanensis*, and *Pseudaelurus validus* (Appendix VII). Any character that could not be scored on a given species was assigned the value of X. In some cases the inability to score a character in a given species was due to high variability of that character. In some cases, the character was not entirely removed from the analysis when variability was present in only a single species. Instead no score was given for the species showing variation and the other species were scored. Each of these matrices was entered into the phylogenetic analysis software PAUP (Phylogenetic Analysis Using Parsimony, Version 4; Sinauer Associates, Sunderland, Massachusetts). A maximum parsimony analysis was run and bootstrap values (each having 1,000 reps) were calculated from the consensus tree of each analysis. To gain a better understanding of the evolution of different characters, the computer program MacClade (Version 4.08a) was used to map the characters on each of the trees (one for each outgroup).

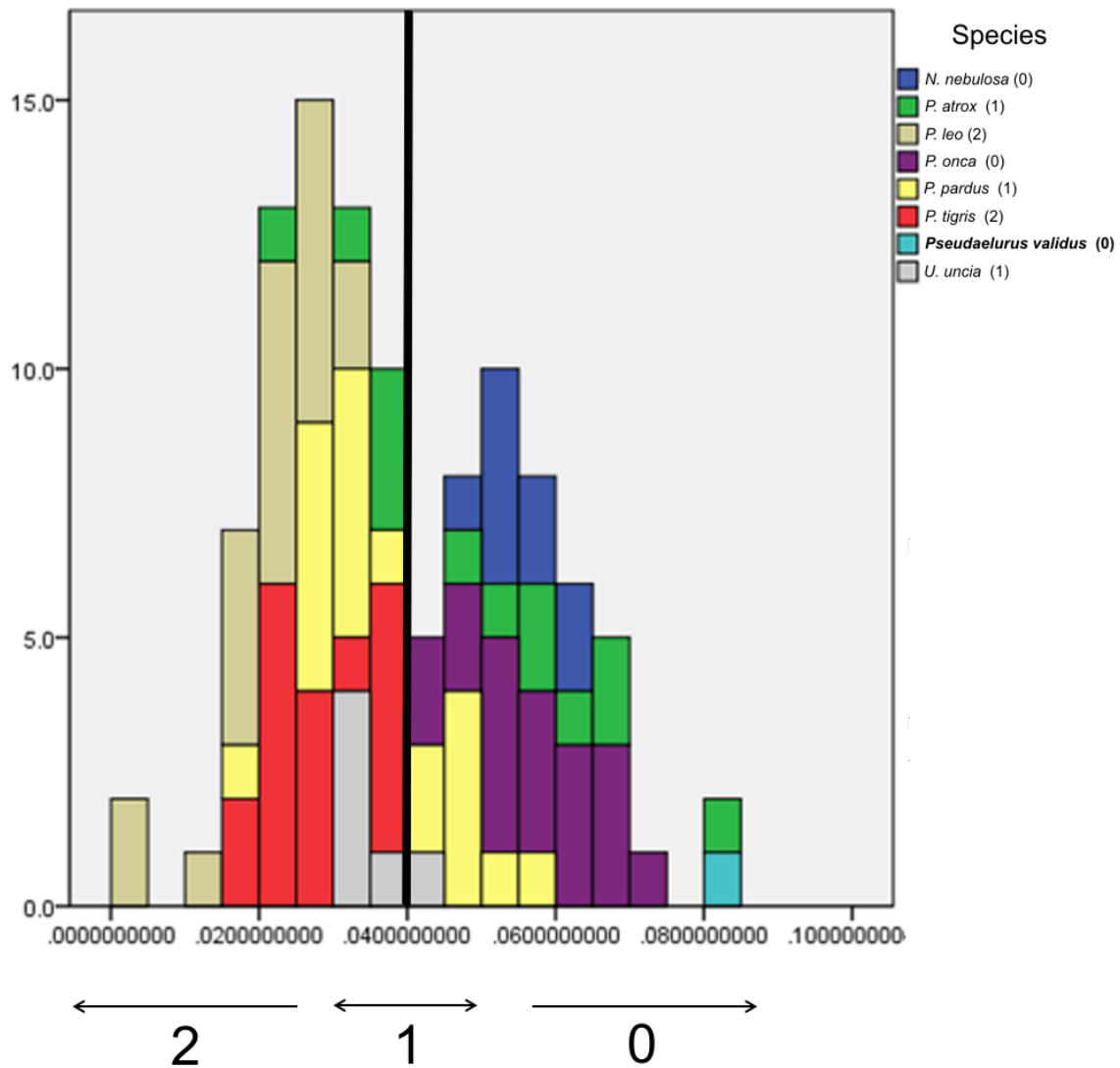


Figure 7. Example of the methodology used when scoring the linear measurements. The outgroup (bold in the legend) is represented by the turquoise specimens and is assigned a score of 0 along with any specimens whose distribution falls entirely to the right of the thick black line. Specimens entirely to the left of the line are assigned a score of 2 and any spanning the line are assigned a 1. The numbers in parenthesis by the species names indicate the score assigned for this particular character.



## CHAPTER 3

### RESULTS

#### Statistical Analyses

##### Crocota crocota

Principle component analysis using *C. crocuta* as the outgroup generated four principle components that together explained approximately 54% of the total variance. A scatter plot of the first two components (Figure 8) did separate each species but with considerable overlap in ranges. Principle component one clearly separated *C. crocuta* from the other species in the analysis. *Panthera atrox* was also separated from the extant species, though not as distinctly. Principle component two created a range with *P. leo* occupying one extreme and *N. nebulosa* occupying the other. All other species fell within this range with a great amount of overlap. The center of this range was occupied by *P. atrox*, *P. tigris*, and *C. crocuta*.

Stepwise discriminant analysis found that 9 of the 13 measurements were statistically significant in separating the different species. These measurements were the angle of the postorbital process to maxilla (character 12), upper canine length (character 27), distance from the postorbital to frontal parietal suture (character 21), distance from the postorbital process to maxillary frontal suture, angle between the hypoglossal and jugular foramina (character 18), angle of the paroccipital process to occipital condyle, angle of the auditory bulla (character 1), ratio of m1 length to width (character 5), and finally the ratio of the P4 length to width (character 41). Each of these measurements was assigned a Wilk's lambda value at or below 0.67. Despite being chosen as significant, the distance from the postorbital process to maxillary frontal suture and angle of the paroccipital process to the occipital condyle were removed from the analysis

due to the histograms being very difficult to divide into character states. Seven discriminant scores were established from the given data, with the first two explaining nearly 80% of the variance. When these two scores are plotted against each other on a scatter plot, it becomes apparent that both clearly separate the outgroup, *C. crocuta*, from the remainder of the species (Figure 9). Along discriminant score one each species does cluster, but there is significant overlap. *Panthera atrox* and *N. nebulosa* make up the two extremes along the X-axis, if *C. crocuta* is not considered. The same pattern holds true along discriminant score two; however, *P. leo* also occupies the same extreme as *P. atrox*.

#### Metailurus ssp.

When *Metailurus* ssp. was used as the outgroup within a principle component analysis three principle components were found to explain approximately 55% of the variance within the measurements for each species. When the first two components were plotted against each other, each species did group accordingly; however, there was a great deal of overlap between species (Figure 10). Along both axes the outgroup plotted in the center of the other points. Because some of the specimens used within the study were only identified as *Metailurus* ssp., a specimen of *M. major* and *M. minor* were included but labeled separately. This was done to account for all possible variation within the genus. All three individuals did plot together, although *M. major* was slightly removed from the others. The first principle component appears to be separating *P. onca* and *P. atrox* from the other species, but this separation is minimal. Separation of species along the second principle component is more defined with *N. nebulosa* being separated from *P. leo* and *P. atrox*. A plot of the second and third principle components once again demonstrated a division of *N. nebulosa* from *P. atrox* and *P. leo* from the second component. Principle component three distinctly divides the outgroup (all species) from the other felids (Figure 10).

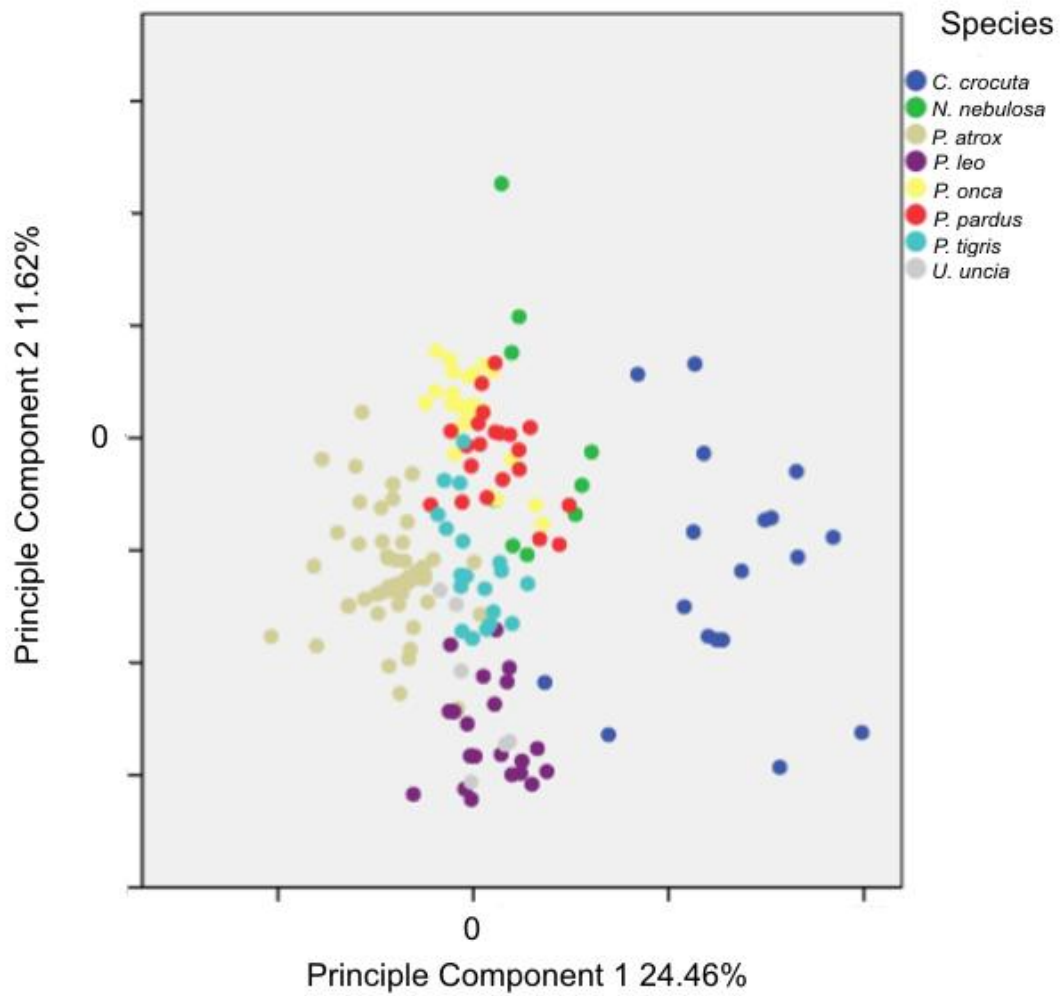


Figure 8. Principle component analysis for the outgroup *Crocota crocuta*. Note the separation along the first principle component of *C. crocuta* from the other species. Principle component two is separating *Panthera leo* from *Neofelis nebulosa*. The third principle component separates *P. leo* and *P. atrox* from the other species.

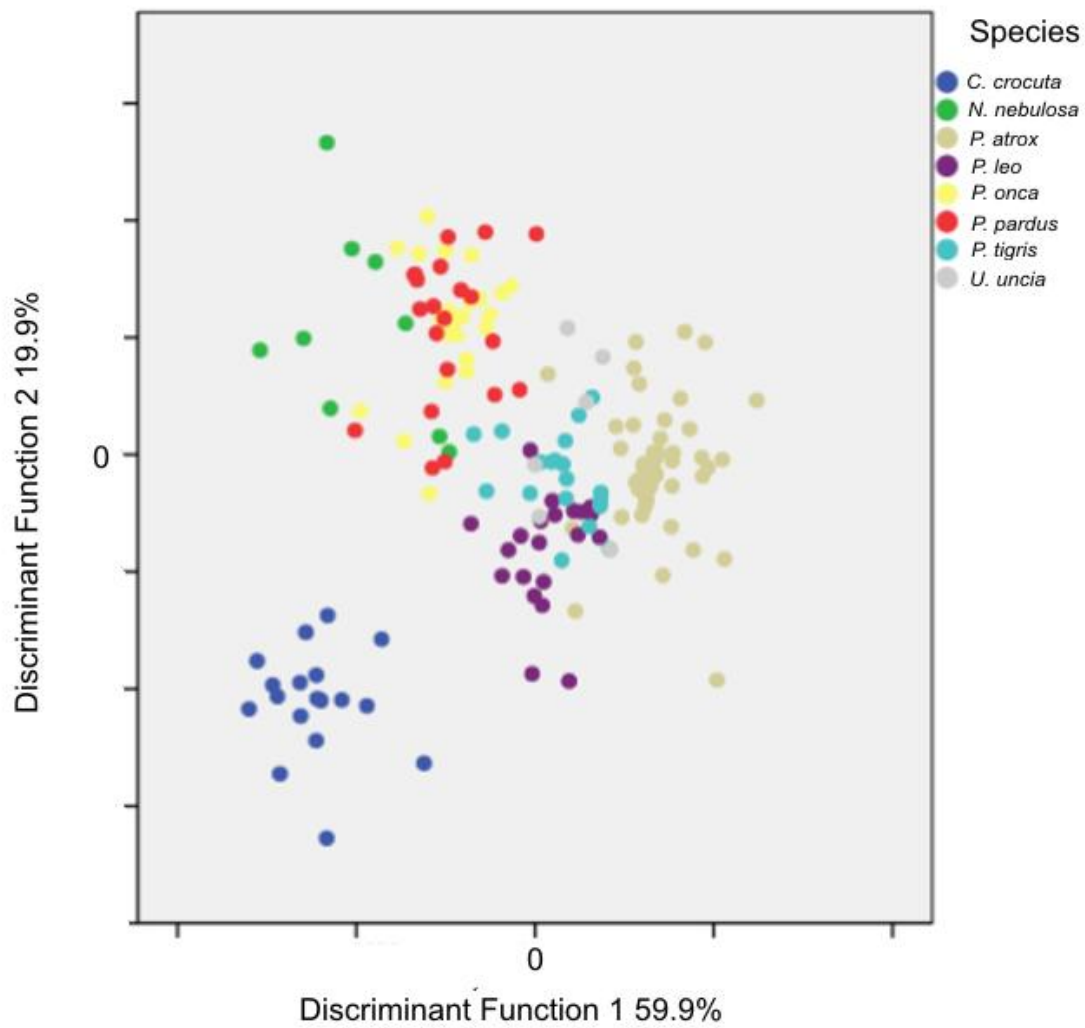


Figure 9. Stepwise discriminant analysis for *Crocota crocuta* as the outgroup. Note that as with the PCA, the first function is separating *C. crocuta* from the other species. The second function also appears to be dividing *C. crocuta* from the other felids. A separation is also present along this axis between *Panthera leo* and *Neofelis nebulosa*.

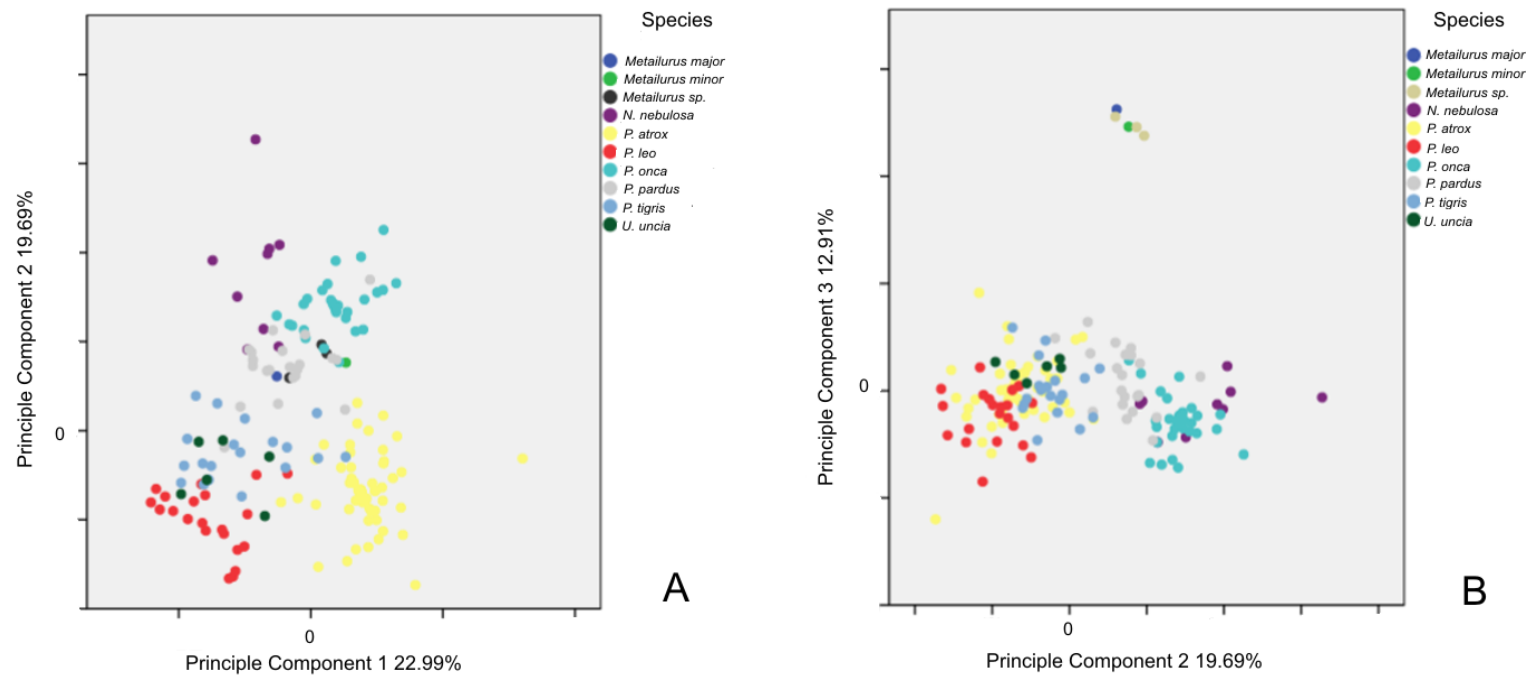


Figure 10. Principle component analyses with *Metailurus* ssp. as the outgroup. The first principle component (A) separates *Panthera atrox* from the other species while the second component (A&B) separates *Panthera leo* and *P. atrox* from *Panthera onca* and *Neofelis nebulosa*. The third principle component (B) separates the specimens within the outgroup from the remaining species.

Of the possible measurements included with *Metailurus* ssp. as an outgroup, 10 out of 12 were significant in the stepwise discriminant analysis. The two characters removed were the angle of the auditory bullae and the length width ratio of the upper carnassial (P4). Each of the retained measurements was assigned a Wilk's lambda value at or below 0.6. Seven discriminant scores were calculated for this analysis, but the first three explain nearly 90% of the variation within the data. On a scatter plot (Figure 11), the first two scores clearly are dividing the outgroup, *Metailurus* ssp., *M. major*, and *M. minor*, from the other felids. Along both axes, the other species group accordingly, but as was seen in the PCA there is a great deal of overlap. The same separation between *N. nebulosa* and *P. atrox* is also seen again in the Stepwise DA (Figure 11).

#### Proailurus lemanensis

PCA with *Proailurus lemanensis* as the outgroup generated three principle components that account for roughly 63% of the data variation. A scatter plot of the first two components places the outgroup in the center of the data on both the X and Y axes (Figure 12). The first principle component appears to be separating the species into two groups; *Panthera onca*, *P. pardus*, and *N. nebulosa* as one group and *P. leo*, *P. tigris*, and *P. atrox* as the other. *Uncia uncia* plots with overlap into both groups. Principle component two is also dividing the species into groups, with *P. leo* and *P. tigris* occupying one end of the range and *P. atrox* and *P. onca* occupying the other end. All other species fall between these two groups with some overlap occurring.

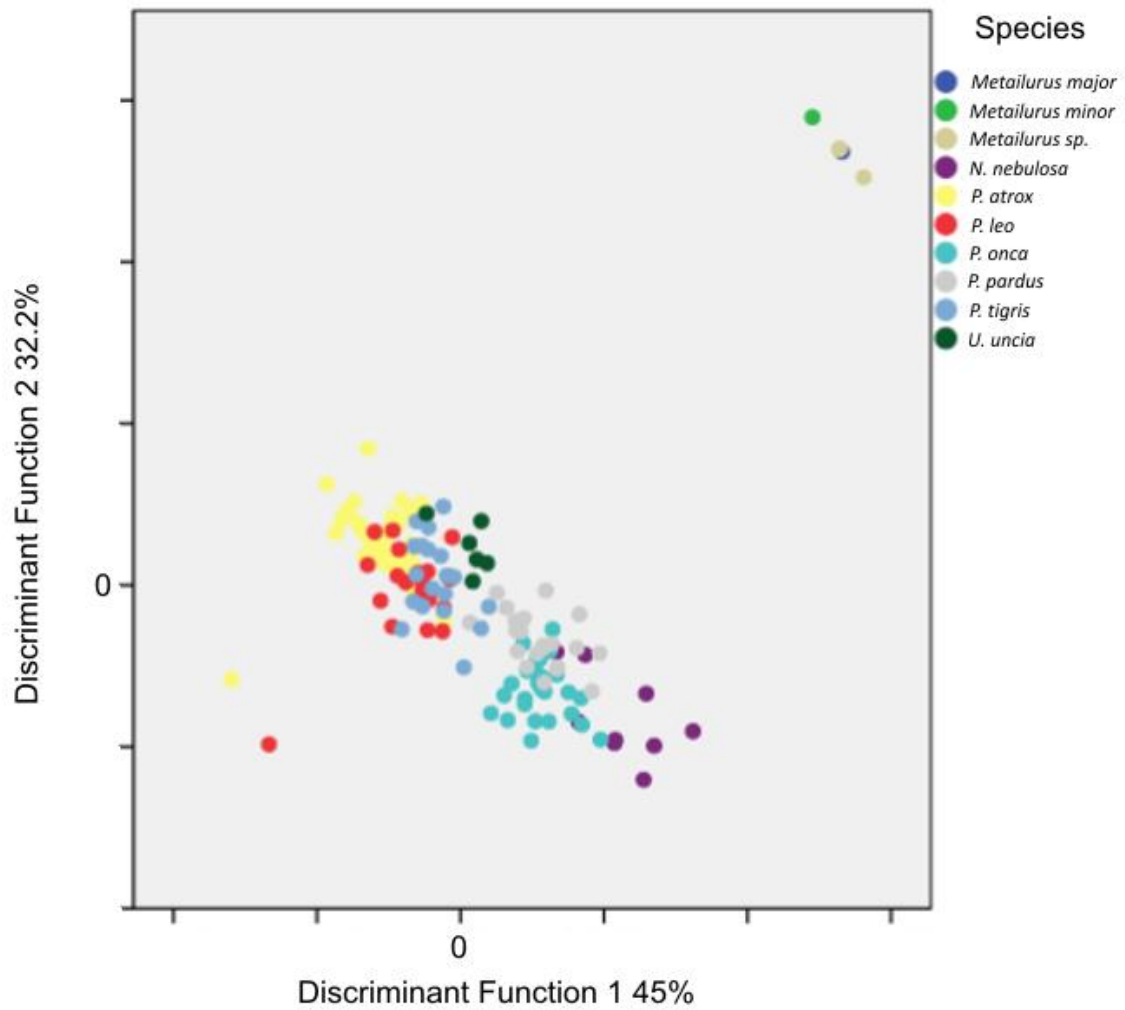


Figure 11. Stepwise discriminant analysis using *Metailurus* as the outgroup. Both discriminant functions clearly separate the outgroup from the other species. Both axes also separate *Neofelis nebulosa* from *Panthera atrox*.

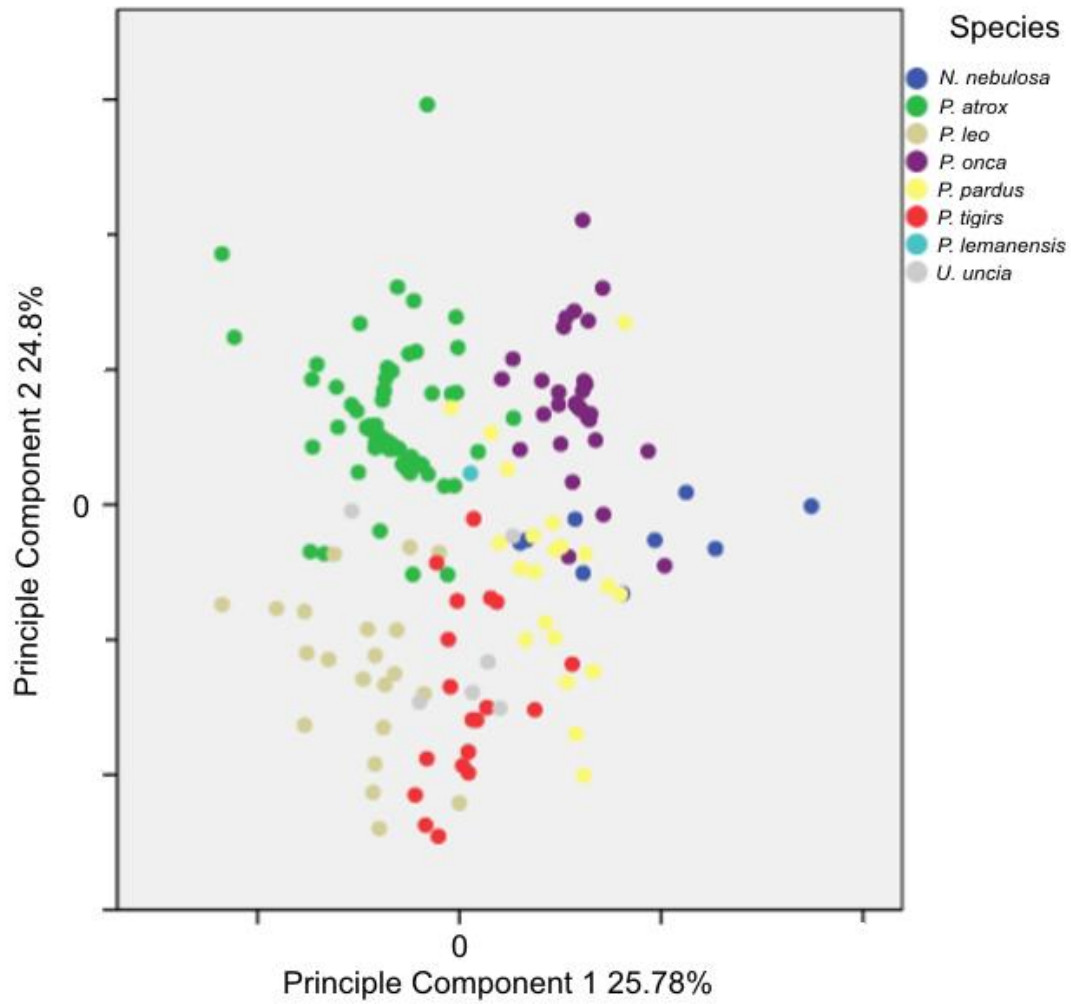


Figure 12. Principle component analysis using *Proailurus lemanensis* as the outgroup. The first principle component separates *Panthera onca*, *P. pardus*, and *Neofelis nebulosa* from *P. leo*, *P. tigris*, and *P. atrox*. Principle component two divides *P. leo* and *P. tigris* from *P. atrox* and *P. onca*.



Stepwise DA considered 8 of the 9 measurements statistically significant. The only measurement removed from the analysis was the length to width ratio of the P4. The measurements included all had a Wilk's lambda score at or below 0.65. Seven discriminant scores were calculated, but the first two account for over 80% of the variation. When these scores are plotted against each other (Figure 13), *Proailurus lemanensis* falls in the center of the graph. Discriminant score one, divides the species into the same two groups seen in the PCA. No overlap is seen with *U. uncia*, however, which instead plots with *Panthera atrox*, *P. leo*, and *P. tigris*. Along discriminant score two, the species are again divided into the same groups as the PCA. However, *N. nebulosa* and *U. uncia* plot entirely within the range occupied by *P. leo* and *P. tigris* instead of overlapping into both groups.

#### Pseudaelurus validus

When *Pseudaelurus validus* was included as the outgroup, the PCA calculated three principle component scores that accounted for 63% of the variation within the data. When the first two scores are plotted against each other (Figure 14), principle component one divides *Panthera atrox* from the other species, though not distinctly, as *P. atrox* still overlaps with other species. The second principle component clearly separates the outgroup, *Pseudaelurus validus*, from the other felids. If *P. validus* is not considered, the second principle component also separates *Panthera leo* and *P. tigris* from *N. nebulosa* and *P. onca*, with overlap of the other species in between.

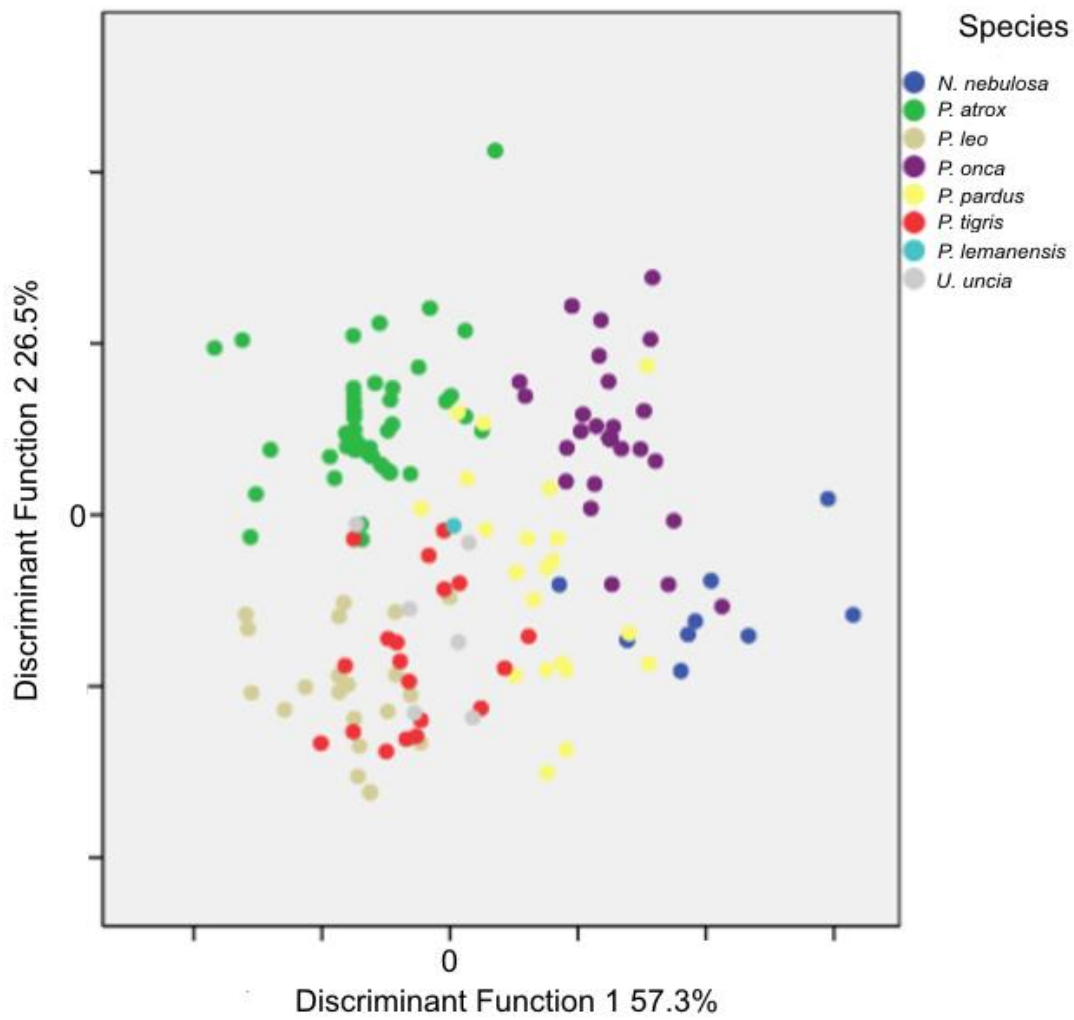


Figure 13. Stepwise discriminant analysis with *Proailurus lemanensis*. Note that discriminant function one divides the species into two groups; *Panthera onca*, *P. pardus*, and *Neofelis nebulosa* from *P. atrox*, *P. leo*, and *P. tigris*. Discriminant function two also divides the species into two groups; *P. leo* and *P. tigris* from *P. atrox* and *P. onca*.

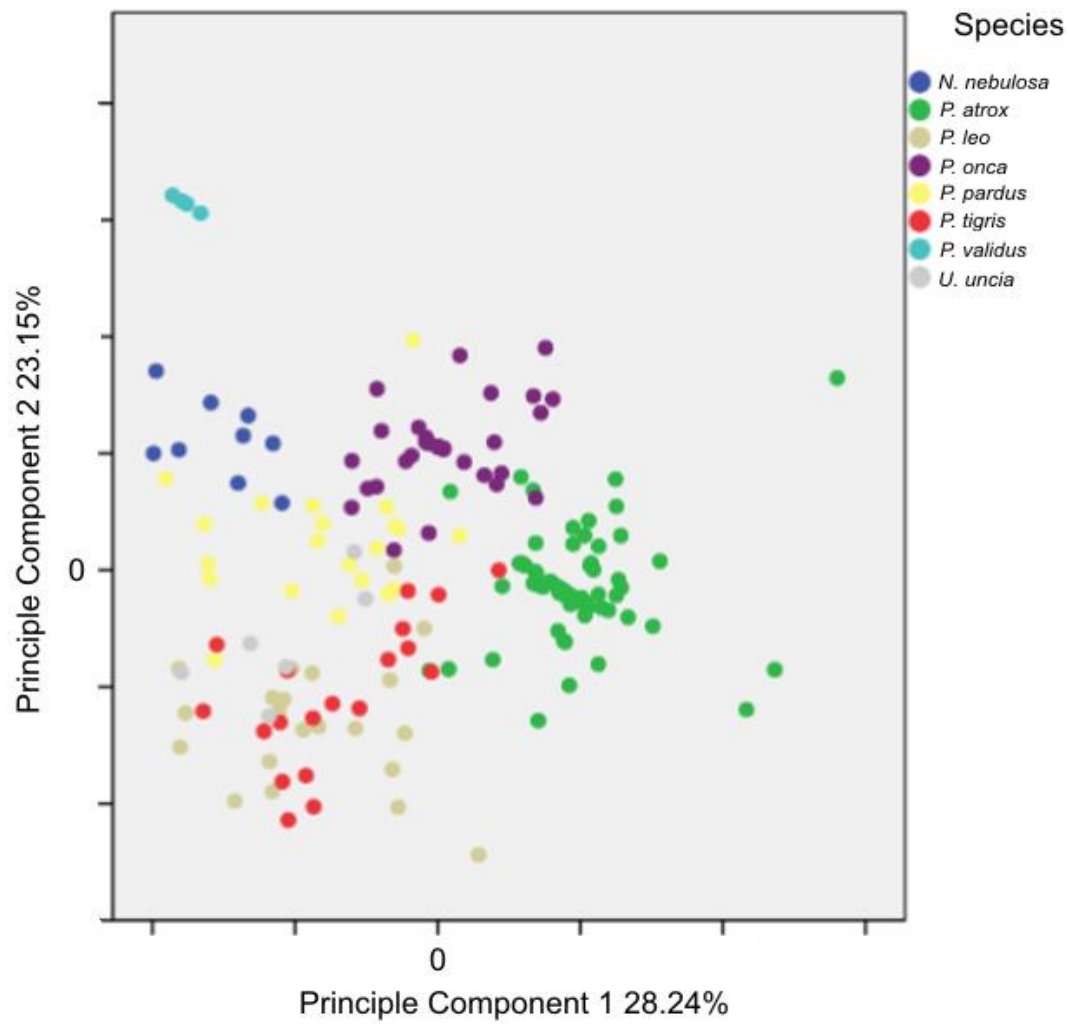


Figure 14. Principle component analysis using *Pseudaelurus validus* as the outgroup. Note that the first principle component separates *Panthera atrox* from the other species, while the second principle component analysis separates the outgroup, *Pseudaelurus validus*, from the other species.

Stepwise DA with *Pseudaelurus validus* included 9 of the 10 possible measurements within the analysis. The character removed was once again the length width ratio of the P4. All other measurements received a Wilk's lambda score at or below 0.559. Once again seven discriminant scores were generated, but the first two account for over 70% of the variation. When these two scores are plotted against each other (Figure 15), the first clearly separates *P. validus* from the other species. Due to this separation, there is considerable overlap within the remaining taxa. However, *Panthera atrox* is still slightly divided from *P. onca* and *N. nebulosa*. Along discriminant score two, *Pseudaelurus validus* falls near the center of the range, with a slight separation present between *Panthera leo* and *P. onca*.

#### No outgroup

Because each PCA appeared to be separating the outgroup from the other species in the analysis, a separate PCA was run excluding any outgroup. The goal of this analysis was to better resolve the groupings of the other felids. The first three principle components created explained just above 56% of the variation within the data. A scatterplot of the first two components (Figure 16) showed a much clearer separation of the felids than was present when an outgroup was included. Such separation is not surprising, as the outgroups highly influenced the plots due to their distinct differences from the other taxa. Each species groups together; however, as was true in the other analyses, overlap is still present. Along principle component one, *Panthera atrox* is separated from the other species, with *N. nebulosa* occupying the opposite end of the spectrum. This same pattern was seen when outgroups were included but is more apparent without them. Principle component two appears to be separating *P. leo* from *P. onca* and *N. nebulosa*, with the other species falling between this division. When the third principle component was plotted (Figure 16), there was no clear separation of species. Instead, the component seemed to be

dividing different individuals of the same species along a spectrum of variation. *Panthera tigris* and *P. pardus* did plot higher on the axis than other species, but there was still considerable overlap.

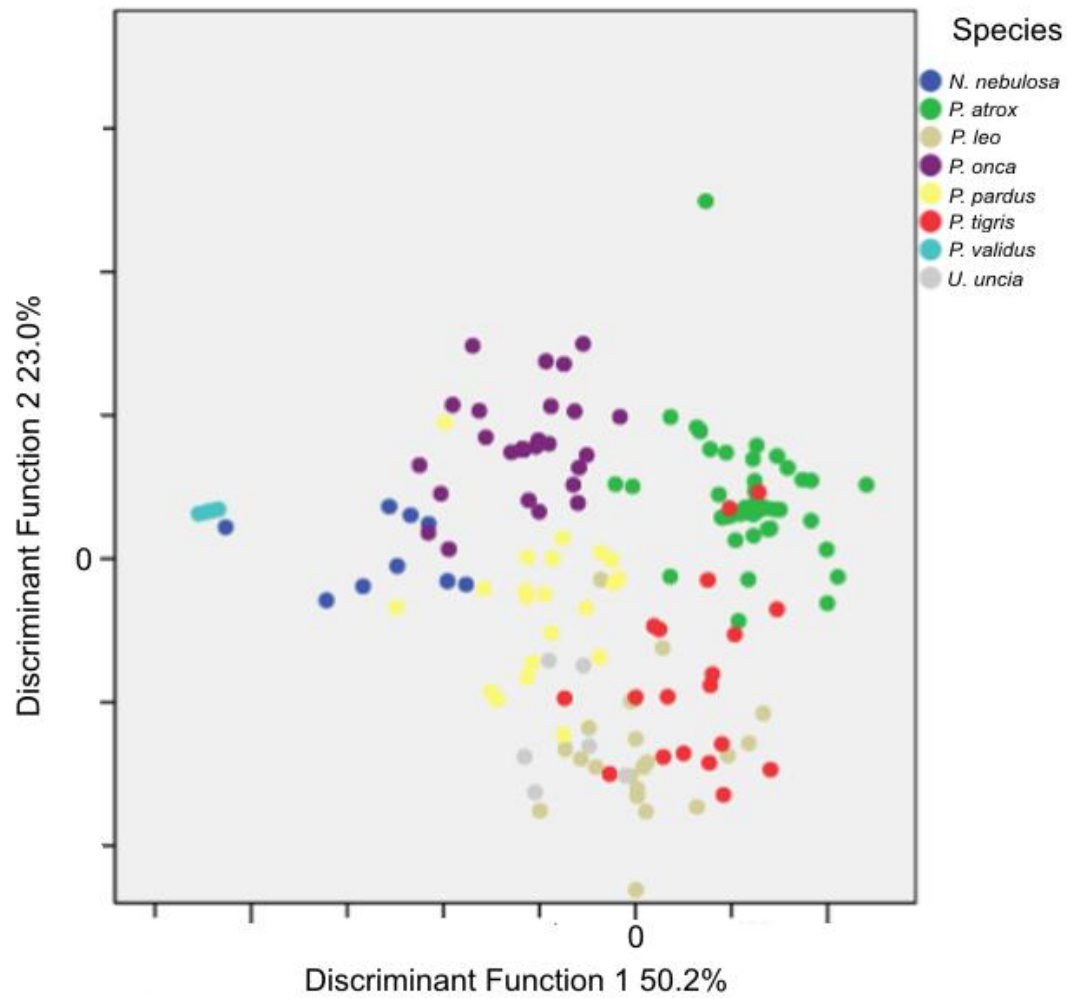
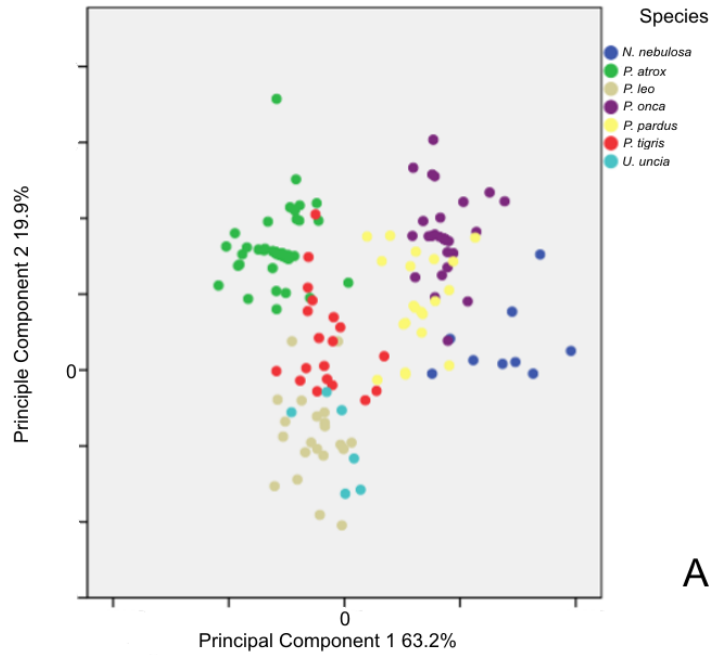
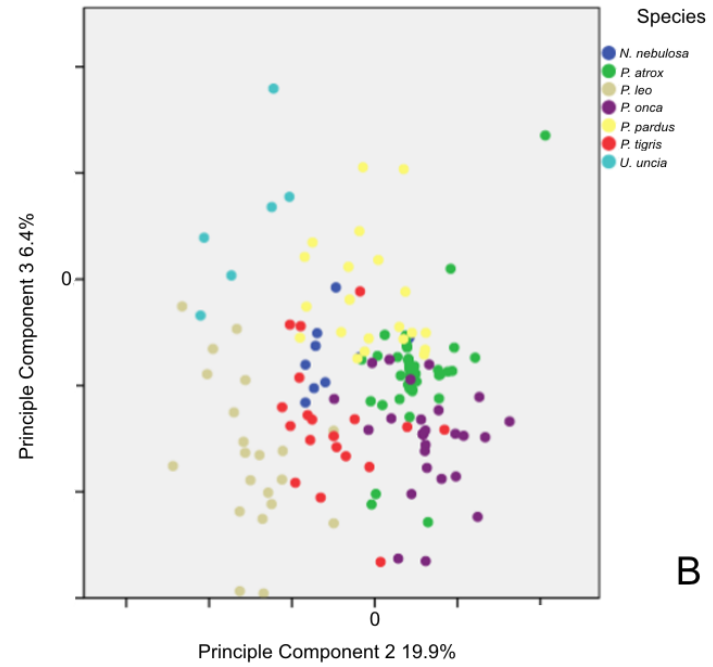


Figure 15. Stepwise discriminant analysis using *Pseudaelurus validus* as the outgroup. Note that the first discriminant function separates the outgroup from the other species. The second discriminant function divides *Panthera atrox* and *Neofelis nebulosa*.



A



B

Figure 16. Principle component analysis not including any outgroup. A) the first principle component separates *Panthera atrox* and *Neofelis nebulosa*, while the second principle component separates *P. leo* from *P. onca* and *N. nebulosa*. B) the second principle component is the same as in the top figure and the third principle component divides different individuals within the same species instead of dividing the different species.

## Phylogenetic Analysis

### Crocota crocuta

After evaluating a total of 10,395 trees, a single most parsimonious tree was retained when *Crocota crocuta* was entered as the outgroup (Figure 17). This single tree has a branch length of 83 and 17 of the characters were determined to be parsimony uninformative. The bootstrap analysis showed that the only statistically supported pairing was between *Panthera pardus* and *N. nebulosa* with a bootstrap value of 53% (Figure 17). *Uncia uncia* is the most basal of the felids within the analysis. Two clades then occur between the remaining species; *P. pardus* and *N. nebulosa* paired as sister taxa to *P. onca*, *P. tigris*, *P. leo*, and *P. atrox*. *Panthera onca* is positioned as the most basal of this group, followed by *P. tigris*, and a sister pairing of *P. leo* and *P. atrox*.

When each individual character was mapped on the tree, it was possible to identify the 17 parsimonious uninformative characters (6, 7, 9, 10, 15, 17, 19, 23, 24, 28, 29, 30, 31, 36, 37, 38, and 41 - Appendix II). Each of these characters represents either an autapomorphy or synapomorphy, so add no information with respect to relationships. The remainder of the characters either develop linearly along the tree or evolve independently multiple times (Figure 18). Character 3 shows a linear evolution from the basal form of a completely tubed auditory meatus in the outgroup to a small projection in all the other felids and finally to a complete loss in *P. atrox*. Character 13, the location of the frontal maxillary suture in relation to the frontal nasal suture, also develops linearly. The primitive state of the frontal nasal being anterior to the frontal maxillary suture is present in the outgroup.



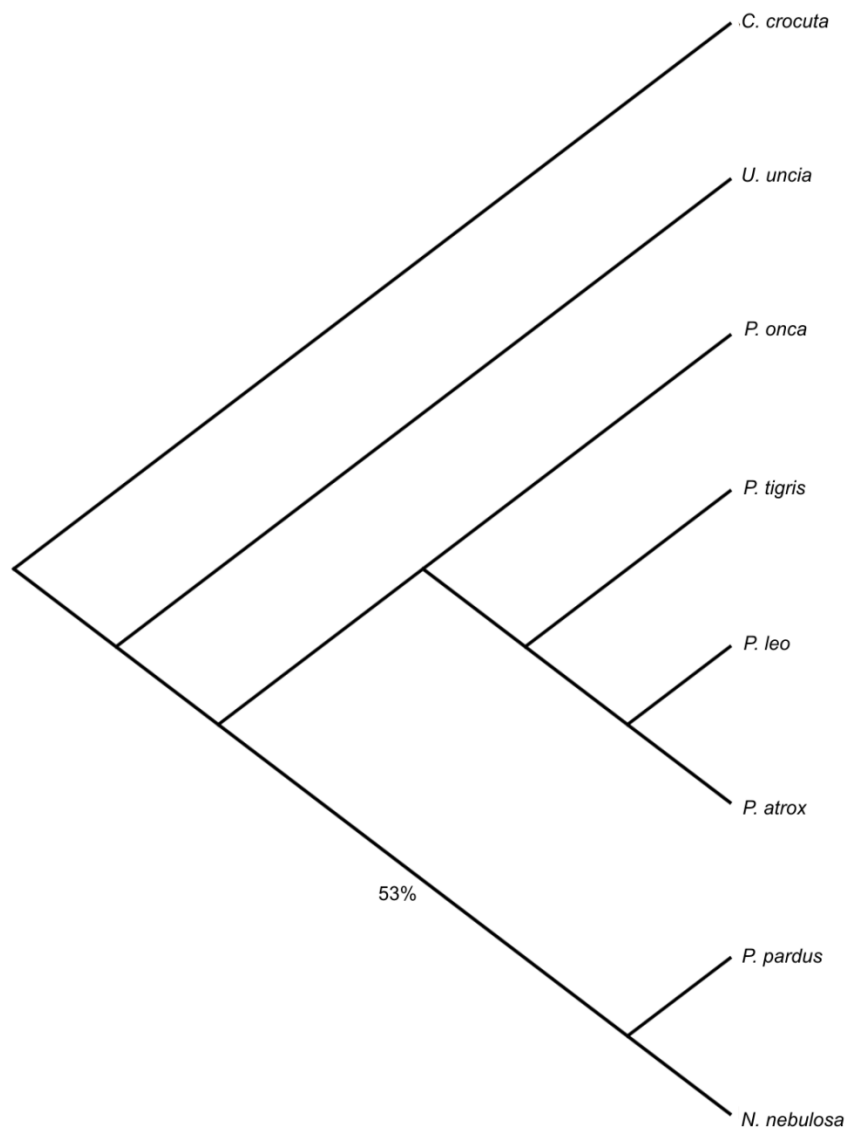


Figure 17. Phylogenetic tree with *Crocuta crocuta* as the outgroup. Note the pairing between *Panthera leo* and *P. atrox*. The relationship between *P. pardus* and *Neofelis nebulosa* has a bootstrap value of 53.

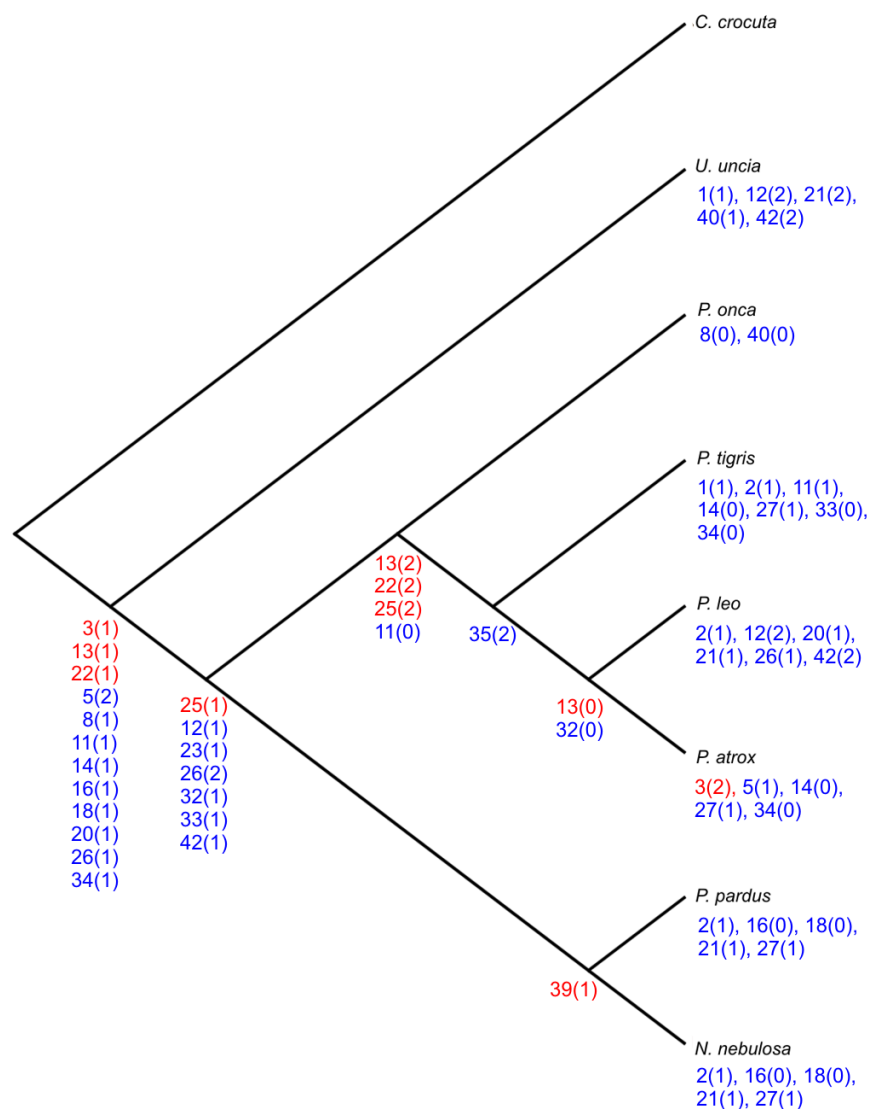


Figure 18. Phylogenetic tree with *Crocota crocuta* as the outgroup. Each character was mapped on the tree and written at the given node where a change occurred. Characters are listed followed by the state in parentheses. Characters that evolve linearly are written in red while those that evolve independently multiple times are in blue.

It then evolves into the two sutures being level in *U. uncia*, *N. nebulosa*, and *P. pardus*. Finally in *P. onca* and *P. tigris* the frontal nasal suture becomes posterior to the frontal maxillary suture and represents the most derived state. However, a reversal appears to occur in *P. leo* and *P. atrox* who once again possess the primitive state. Character 22, the ratio of the distance between the postorbital process and the frontal parietal suture to skull length, is another character that evolves linearly. The primitive state is only present in the outgroup, while the next state appears in *U. uncia*, *N. nebulosa*, and *P. pardus*. The most derived state then appears in the remainder of the species. Character 25, development of the parastyle on P3, is also linear, being absent in *C. crocuta* and *U. uncia*, minor in *P. pardus* and *N. nebulosa*, and finally well developed in the remainder of the taxa. Similar developments were also noted by Salles (1992). The final character to evolve linearly along the tree is character 39, the presence of a reduced or nonreduced paroccipital process. All species within the analysis have the primitive state where the paroccipital process is present and not reduced except the node containing *N. nebulosa* and *P. pardus*, who have a highly reduced paroccipital process. All other characters within the analysis have states that develop independently multiple times along the tree. For example, character 2, where the process between entotympanic and ectotympanic (above vidian nerve canal) does not or does protrude ventrally, has the derived state of not protruding appearing three times independently. These appearances occur in *P. onca*, *P. pardus*, and *P. leo*, suggesting these characters could represent convergent character states.

#### Metailurus ssp.

When *Metailurus ssp.* was used as the outgroup, PAUP again evaluated a total of 10,395 trees, but retained three most parsimonious trees. Each tree had a branch length of 74, and 10 characters were defined as parsimony uninformative. When bootstrap values were run on the

consensus tree, no pairings were statistically supported by more than 50% (Figure 19D). The first tree placed *U. uncia* as the most basal taxon, aside from the outgroup (Figure 19A). *Neofelis nebulosa* occupies the next most derived position. *Panthera onca* and *P. pardus*, which are paired as sister taxa, are divided from *P. tigris*, *P. leo*, and *P. atrox*. Within the latter group, *P. tigris* is the more basal, while *P. atrox* and *P. leo* are the more derived sister taxa. The second tree shows a very linear evolutionary history, with *U. uncia* being the most basal felid, excluding the outgroup, and *P. atrox* and *P. tigris* being the most derived sister taxa (Figure 19B). The other species fall between in the following order: *N. nebulosa*, *P. onca*, *P. pardus*, *P. leo*. The third tree resembles the first tree with *U. uncia* as the most basal and *P. onca* and *P. pardus* being a highly derived pairing (Figure 19C). *Panthera tigris* and *P. atrox* are also sister taxa and are paired at the same level as *P. pardus* and *P. onca*. *Panthera leo* is placed at the node following *U. uncia* and is then followed by *N. nebulosa*. When a consensus was made of these three trees it became apparent that there was difficulty in discerning the relationship between *P. onca*, *P. pardus*, *P. leo*, *P. tigris*, *P. atrox*, and *N. nebulosa* as they were each plotted sharing the same node (Figure 19D).

After tracing the characters using MacClade, it was determined that characters 1, 2, 4, 7, 8, 16, 25, 26, 29, and 34 were parsimonious uninformative (Appendix III). Because three trees were created for this analysis, it was necessary to trace characters on all three trees to determine which characters evolve linearly and which arise independently. It was also then necessary to compare any differences between the three trees (Figure 20). Character 3, the presence, reduction, or absence of the metaconid on m1, evolves linearly in all three trees. *Panthera tigris*, *P. atrox*, *P. pardus*, and *P. onca* have all lost the extra cusp, while *U. uncia*, *N. nebulosa*, and *P. leo* have a reduced metaconid.

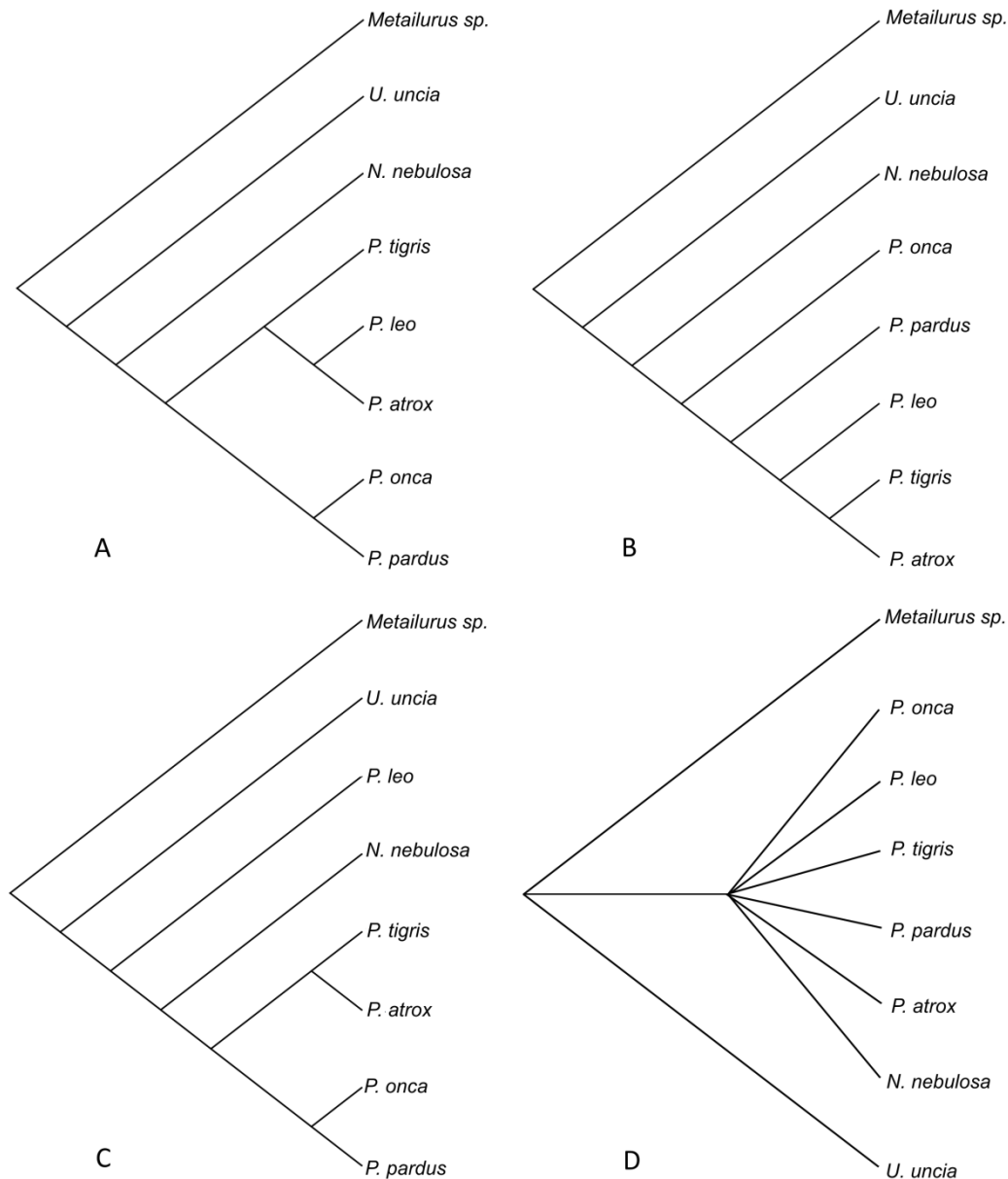


Figure 19. Phylogenetic trees created when *Metailurus ssp.* was used as the outgroup. In all of the trees *Uncia uncia* is the most basal pantherine. A) note the pairing of *Panthera leo* and *P. atrox* with *P. tigris* as a sister taxon. B) the relationship between *P. leo*, *P. tigris*, and *P. atrox* is still present, however, in this tree *P. atrox* and *P. tigris* are sister taxa. C) the same pairing of *P. atrox* and *P. tigris* is present. D) consensus tree from the three different trees created show a difficulty in discerning the relationship between all the species except *U. uncia*.

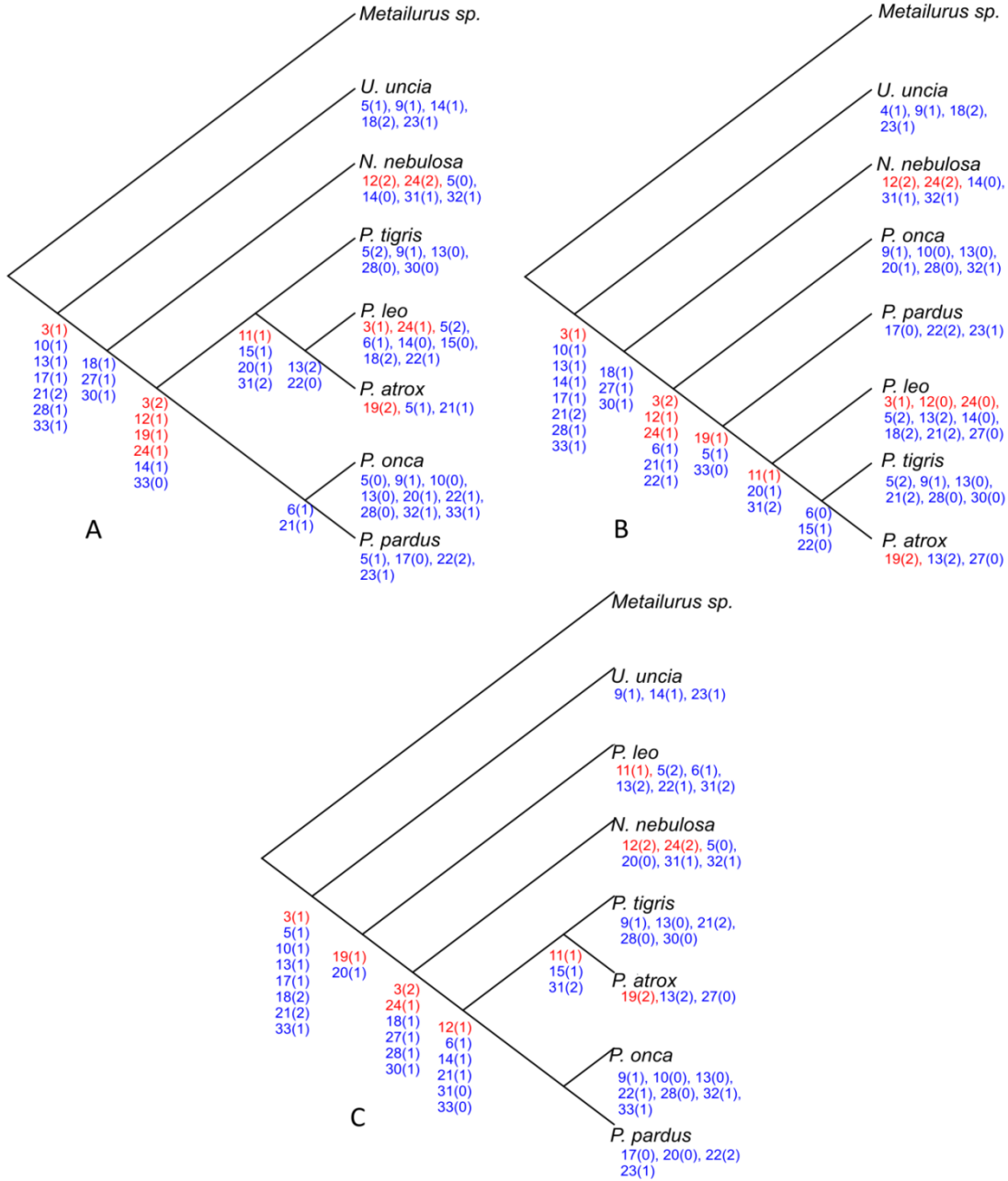


Figure 20. Phylogenetic trees with *Metailurus* spp. as the outgroup. Each character was mapped on the tree and written at the given node where a change occurred. Characters are followed by the state in parentheses. Characters that evolve linearly are written in red whereas those that evolve independently multiple times are in blue.

In trees one and two, however, *P. leo* shares a node with *P. tigris*, *P. atrox*, *P. pardus*, and *P. onca*. Character 11, the intersection between the foramen ovale and pterygoid process of the basisphenoid, is absent in *P. leo*, *P. tigris*, and *P. atrox*. However, in tree three because *P. leo* does not share the same node as *P. tigris* and *P. atrox*, the loss of an intersection arises independently in *P. leo*. Character 12 evolves linearly only in tree three. In this character, the angle between the maxilla and postorbital process is greater than 90° (primitive state) in the outgroup *Metailurus* ssp., *U. uncia*, and *P. leo*. It then develops between 80°-115° in *P. tigris*, *P. onca*, *P. pardus*, and *P. atrox*, until finally reaching an angle less than 90° in *N. nebulosa*. Trees one and two exhibit the same pattern; however, the placement of *P. leo* suggests the occurrence of an independent development of the ancestral state. The ratio of the distance between the postorbital process and the frontal parietal suture to skull length, character 19, also evolved linearly with the ancestral state present in *Metailurus* ssp., *U. uncia*, and *N. nebulosa*. *Panthera atrox* is then the only species to possess the most derived state is then present only in *P. atrox*. In tree three, this development is partially unresolved due to the placement of *P. leo* and *N. nebulosa*. Character 24, the ratio of the upper canine length to skull length, exhibits the same pattern of evolution as character 3, with the most derived state again only present in *N. nebulosa*. All other characters either have states that arise independently multiple times or show a potential reversal in evolution with state two appearing before state one.

#### *Proailurus lemanensis*

Of 10,395 trees considered, three most parsimonious trees were retained when *Proailurus lemanensis* was designated as the outgroup. Each of the three trees has a branch length of 47 and 13 characters were deemed parsimony uninformative. An 80% bootstrap value was present for the clade including all of the species except *P. lemanensis* and *U. uncia* (Figure

21D). A value of 76% was also assigned to the grouping of *Panthera pardus*, *P. onca*, *P. tigris*, *P. leo*, and *P. atrox*. The first two trees show a linear evolution with *U. uncia* as the most basal and *P. leo* as the most derived (Figure 21A-B). *Panthera leo* is placed as a sister taxon to either *P. tigris* or *P. atrox*, depending on the tree. In tree one *P. tigris* is the sister taxon to *P. leo*, making *P. atrox* the sister taxon to this pairing. The opposite arrangement then occurs in tree two. After *U. uncia*, the other species were placed in the following order: *N. nebulosa*, *P. pardus*, and *P. onca*. Tree three also places *U. uncia* as the most basal species followed by *N. nebulosa* and *P. pardus* (Figure 21C). Two clades then occur, placing *P. leo* and *P. atrox* as sister taxa and *P. tigris* and *P. onca* as another sister pairing. All four species represent the most derived within the analysis. The consensus tree shows an inability to discern the relationship between *Proailurus lemanensis* and *U. uncia* (Figure 21D). *Neofelis nebulosa* and *Panthera pardus* have clearly defined nodes that are supported by the bootstrap values at each. The consensus then groups *P. onca*, *P. leo*, *P. tigris*, and *P. atrox* at the same node. When each character was traced on the three trees produced, characters 1, 3, 4, 5, 9, 11, 15, 16, 17, 22, 23, 27, 28 were parsimonious uninformative. Of the remaining characters, only four evolve linearly on all three trees (Figure 22). The first, character 8, represents the ratio of the m1 length to width. All of *Panthera*, which share a node in each tree, possess the more derived state of this character. Character 12, the intersection of the pterygoid process of the basisphenoid with the foramen ovale, is only present in *P. leo*, *P. atrox*, and *P. tigris*, which share a node in trees one and two. In tree three, this relationship is lost due to *P. tigris* being placed as a sister taxon to *P. onca*. Character 18, the location of the posterior palatine foramen in relation to the carnassials, evolves linearly in all three of the trees. The primitive location, anterior to the carnassial, was only present in the outgroup. *Panthera pardus*, *N. nebulosa*, and *U. uncia* all possess the foramen posterior to the



carnassials but anterior to the carnassial notch, while exhibiting the more derived trait of the foramen posterior to the carnassial notch is present in *P. atrox*, *P. leo*, *P. tigris*, and *P. onca*. Character 20, the development of the parastyle on P3, also evolves linearly and much the same as character 18. However, *U. uncia* is an exception in having primitive state. As with the other analyses, the remaining characters have traits that arise independently multiple times.

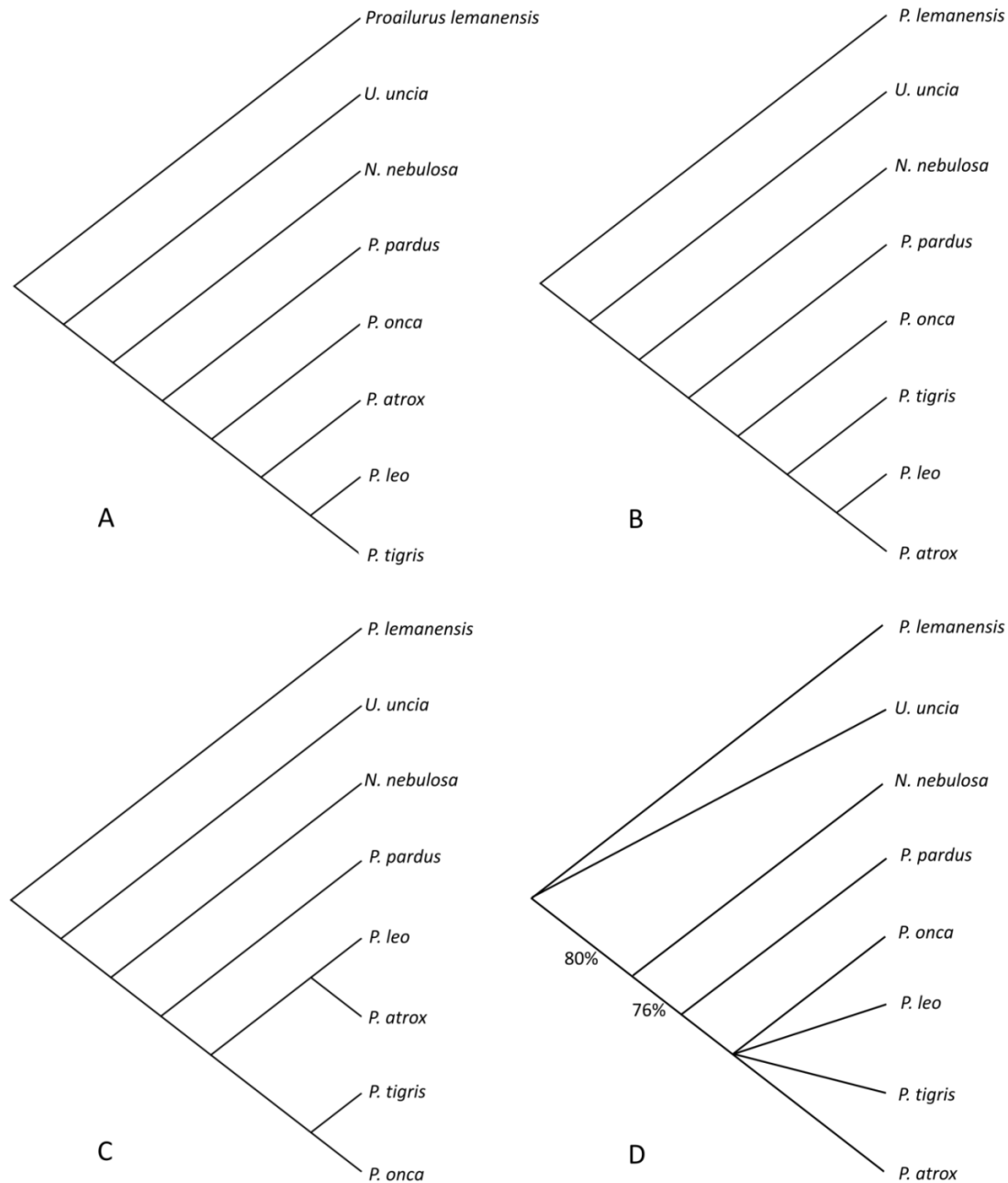


Figure 21. Phylogenetic trees created using *Proailurus lemanensis* as the outgroup. All trees consistently have *Uncia uncia* and *Neofelis nebulosa* as the most basal pantherines. A) *Panthera atrox* is an basal to the sister pairing of *P. leo* and *P. tigris*. B) the same relationship between *P. leo*, *P. tigris*, and *P. atrox* is present, however, *P. leo* and *P. atrox* are sister taxa. C) *P. leo* and *P. atrox* are paired again as sister taxa. D) consensus tree has an 80% bootstrap value supporting the relationship of *U. uncia* as the most basal pantherine. A 76% bootstrap value supporting *N. nebulosa* as the next most derived species. There is an inability to determine relationships within *Panthera*, however, *P. pardus* does act as the most basal member.

## Pseudaelurus validus

When *Pseudaelurus validus* was included as the outgroup, six most parsimonious trees were created after evaluating 10,395 possibilities. Each tree has a branch length of 61 and contains 10 parsimonious uninformative characters. A bootstrap value of 55% supported *U. uncia*'s placement as basal to *Panthera* and 53% supported *P. validus* and *N. nebulosa*'s placement as basal to all the taxa in the analysis (Figure 23F). Tree one places *N. nebulosa* as the most basal species in the analysis, excluding the outgroup, followed by *U. uncia* (Figure 23A). Two clades then occur with *Panthera leo* and *P. tigris* placed as sister taxon to *P. atrox*, *P. onca*, plus *P. pardus*. Within the latter, *P. atrox* is basal to *P. onca* and *P. pardus*. The second, fourth, and fifth trees all show a simple branching pattern of species; however, the order of such evolution varies greatly. Within the second tree, *P. onca* is the most basal and *P. leo* and *P. atrox* are the most derived species (Figure 23B). Remaining species fall between them in the following order: *U. uncia*, *N. nebulosa*, *P. pardus*, *P. tigris*. Tree three places *N. nebulosa* and *U. uncia* as the more basal species, followed again by two separate clades. The first pairing occurs between *P. atrox* and *P. leo* and the second includes *P. tigris*, *P. onca*, and *P. pardus*. The latter group has *P. onca* and *P. pardus* as sister taxa with *P. tigris* basal. Tree four varies from the second by having *N. nebulosa* followed by *U. uncia*, *P. tigris*, *P. leo*, *P. atrox*, and then the *P. onca*-*P. pardus* sister group (Figure 23D). Tree five alternates the position of *P. leo* and *P. tigris*, but the group including *P. atrox*, *P. onca*, and *P. pardus* is still present (Figure 23E). As can be expected, the consensus tree shows little differentiation in the relationships of the felids analyzed here (Figure 23F). However, the position of *U. uncia* as basal to the *Panthera* is consistent and supported by bootstrap values, though not with greater than 75% confidence. The evolutionary relationships within *Panthera* cannot be determined, as is evident by the five species sharing a

single node. However, the placement of each of the species within *Panthera* is supported with a 55% bootstrap value.

The 10 characters deemed parsimonious uninformative after each character was mapped on the tree were character numbers 5, 9, 11, 12, 13, 21, 26, 27, 28, and 29. Of the remaining characters, two (4 and 15 - Figure 24) consistently evolved linearly on all five trees. Character 4, the ratio of the m1 length to width, is derived in all the species within *Panthera*, which all share a common node. Character 15, the smallest ratio of the distance between the postorbital process and the frontal parietal suture to skull length, is also derived within *Panthera*, with *P. atrox* possessing the most derived state. Other characters (17 and 19) develop linearly in a single tree, but are not consistent within the remaining four trees. . However, character 17 appears to develop state 2 before state 1. The remaining 14 characters develop states independently and vary considerably based on the tree in question.

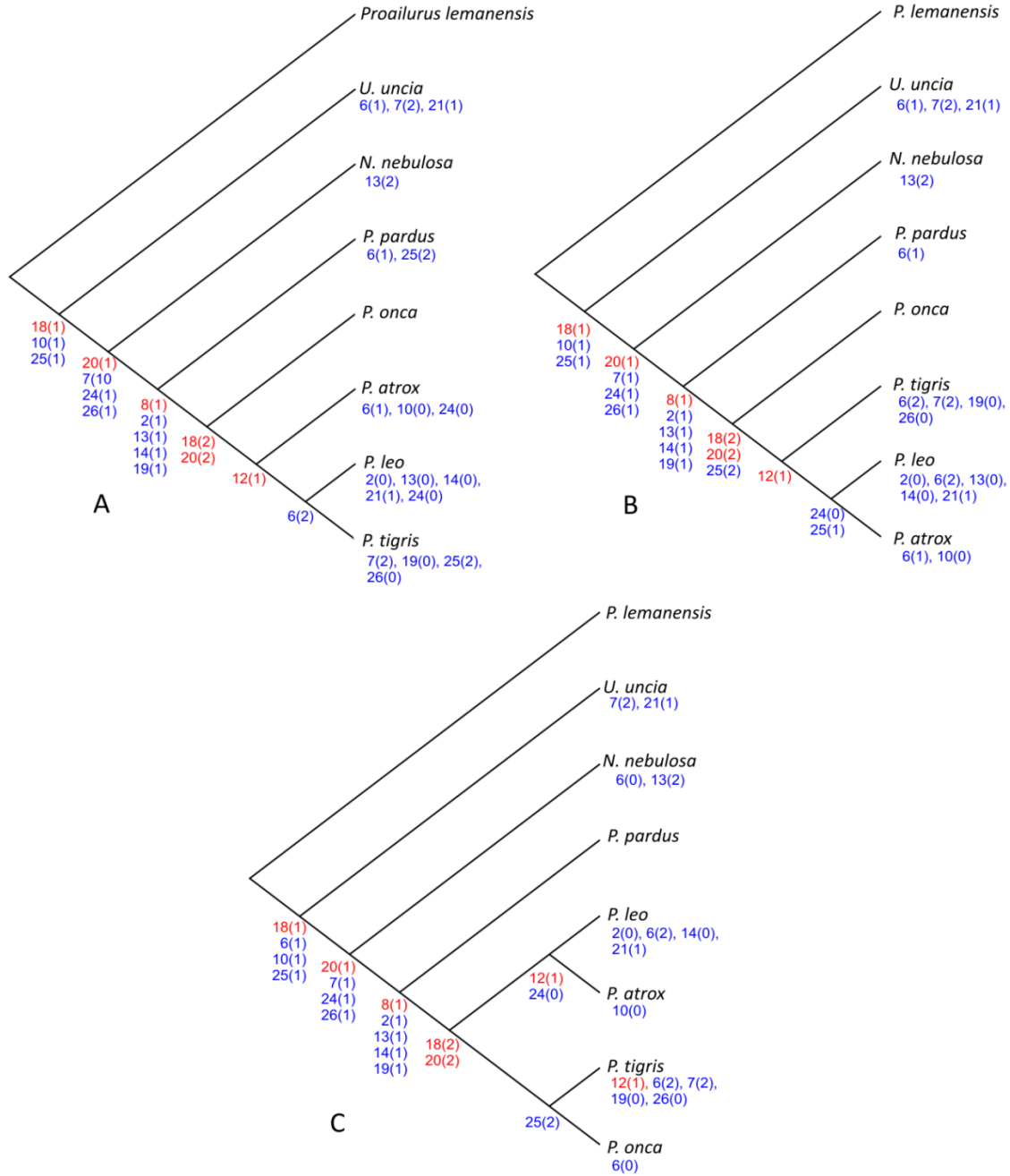


Figure 22. Phylogenetic tree with *Proailurus lemanensis* as the outgroup. Each character was mapped on the tree and written at the given node where a change occurred. Characters are followed by the state in parentheses. Characters that evolve linearly are written in red while those that evolve independently multiple times are in blue.

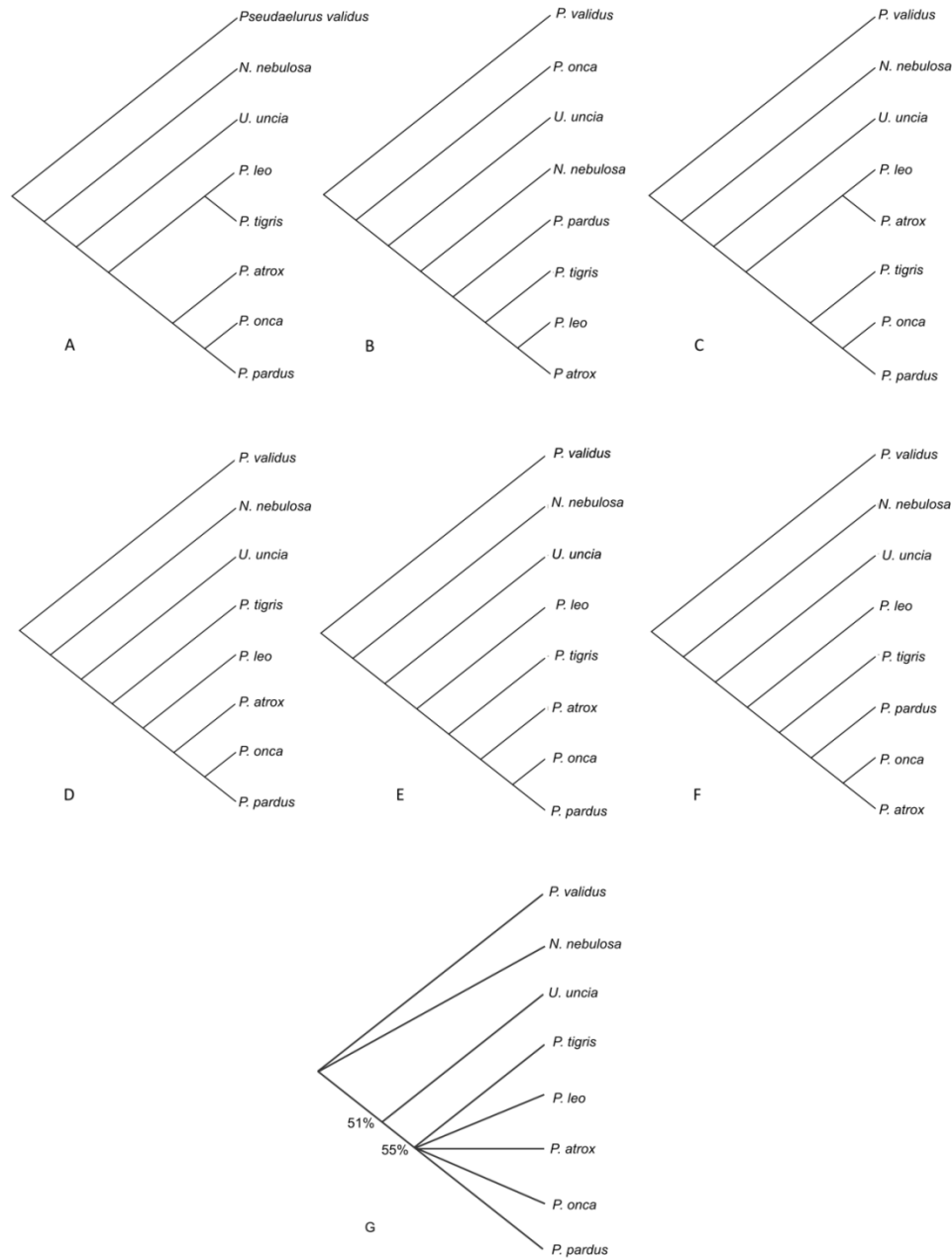


Figure 23. Phylogenetic trees created when *Pseudaelurus validus* was used as the outgroup. All trees have *Neofelis nebulosa* and *Uncia uncia* as the most basal pantherines. A) *Panthera atrox* is basal to the sister taxa *P. onca* and *P. pardus*, B) the same relationship for *P. atrox* is present, however, *P. tigris* and *P. leo* are no longer paired, C) *P. atrox* is a sister taxon to *P. leo*, D) again *P. atrox* is basal to *P. onca* and *P. pardus*, E) *P. atrox* is a sister taxon to *P. onca* while *P. pardus* is basal to the pair, F) the consensus tree created from the five different trees have a 62% bootstrap value supporting the basal relationship of *N. nebulosa*. *U. uncia* is basal to *Panthera*, and no relationship was clear within the latter.

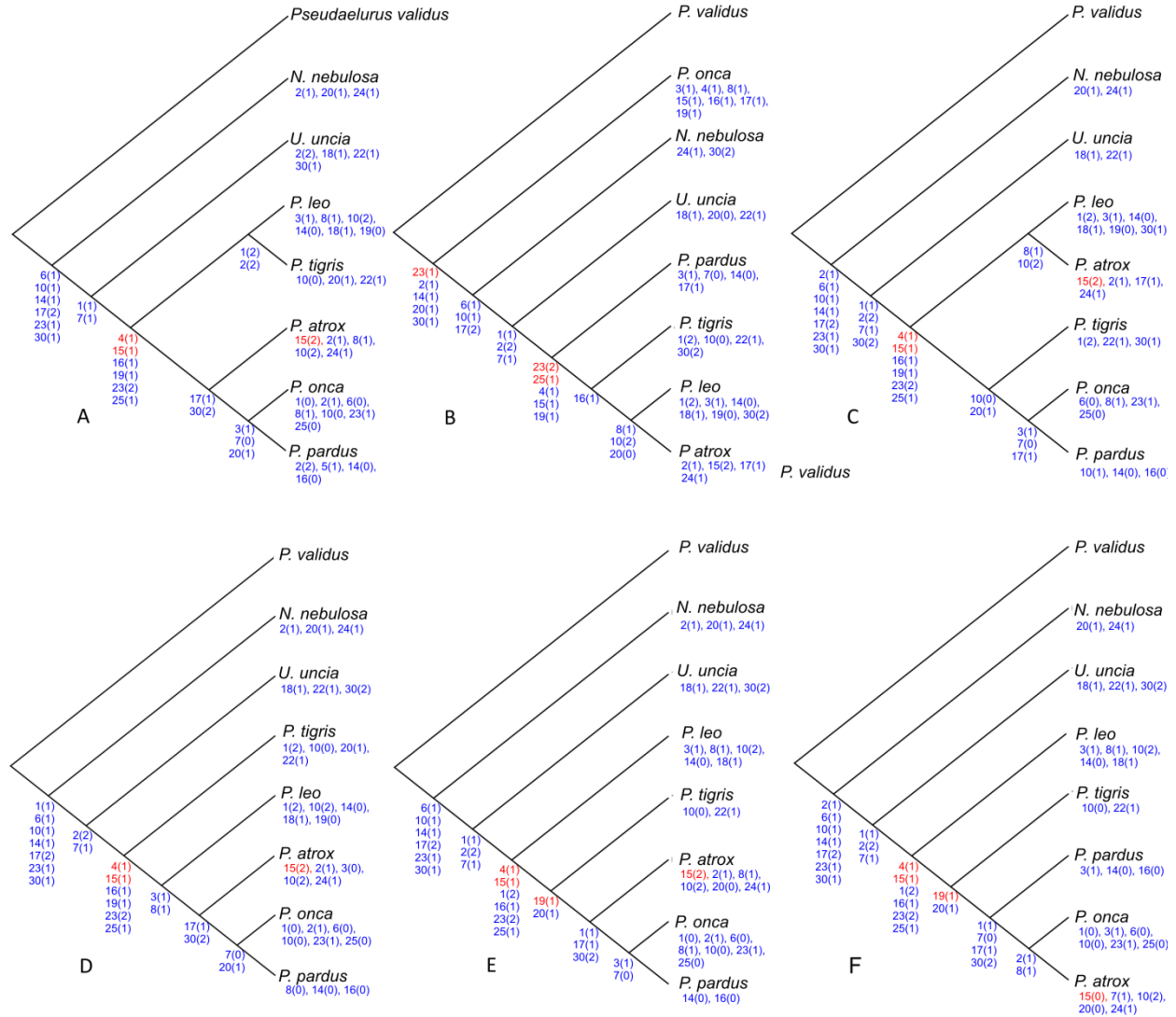


Figure 24. Phylogenetic tree with *Pseudaelurus validus* as the outgroup. Each character was mapped on the tree and written at the given node where a change occurred. Characters are written with the character number followed by the state in parentheses. Characters that evolve linearly are written in red while those that evolve independently multiple times are in blue.

## CHAPTER 4

### DISCUSSION

#### Linear measurements

Several of the linear measurements made on each skull were statistically significant in separating the different species through the Stepwise DA. In order to better understand this significance, it is necessary to access what each character represents and why it is important. The first character of significance is the angle between the maxilla and postorbital process, which represents the angle of the rostrum and mouth in relation to the top of the orbits. A larger angle would suggest the nose points ventrally when the head is held horizontally, while a smaller angle would suggest an dorsal rotation of the rostrum. Higher angle measurements were seen in *Panthera leo*, *P. tigris*, and *U. uncia*, which is consistent with a more ventral placement of the rostrum on these cats in comparison to other members of *Panthera*.

Upper canine length in relation to the skull length was also significant. Upper canine length could represent an affinity toward a “saber-toothed” method of prey capture, with the canines responsible for the final bite to the jugular. The highest ratios for this measurement were in *P. onca*, *P. pardus*, and *N. nebulosa*. All of these felids are ambush hunters that heavily rely on their bite to take down prey (Guggisberg 1975; Turner and Anton 1997; Haas et al. 2005). It has also been proposed that *N. nebulosa* shares similarities with machairodonts, enough so it was originally thought the two were related (Turner and Anton 1997). Such similarities may suggest these cats have a hunting style convergent with that of the extinct saber-toothed felids. Other measurements such as the distance of the frontal parietal suture from the postorbital process could indicate shortening or lengthening of the braincase. *Panthera onca*, *P. atrox*, and *P. tigris*



had the longest braincases. Changes in the braincase may suggest a shift in importance of hearing (larger auditory region) or simply changes in brain size. Because *P. onca* and *P. tigris* both are commonly found in forested habitats and rely on hearing more so than smell for hunting (Nowak 1999), this reliance could be what is reflected in the lengthening of the braincase. Because *P. atrox* also shares this trait, it is possible it was implementing similar hunting strategies. Distance between the postorbital process and frontal maxillary suture also proved to be an important character. Those species with the highest ratios were *U. uncia*, *P. pardus*, and *P. atrox*. When compared to the other pantherine cats, these species have relatively large orbits and in life appear to have much larger eyes in relation to the size of their skulls. It is, therefore, possible that in life, *P. atrox* resembled the eye size of these modern cats.

Differences or similarities in the teeth between species could represent differences in prey or hunting styles and may not entirely be related to phylogeny. For example, the ratio of length to width of the lower and upper carnassials (m1 and P4 respectively) were both chosen as significant. A wider tooth, and thus smaller ratio, may mean the tooth is being used slightly less for shearing of meat, but instead for harder material (perhaps even bone, as is seen in *C. crocuta*). A thinner tooth would appear more blade-like and is likely used for shearing of meat. The most robust teeth were seen in *N. nebulosa*, *P. pardus*, and *P. tigris*. However, these measurements were still low in comparison to *C. crocuta* and *Pseudaelurus validus*. Dominguez-Rodrigo (1999) found that lions leave tooth markings on the bones of prey after defleshing. However, the bones with the greatest damage were those often associated with having the most meat (Dominguez-Rodrigo 1999). *Crocuta crocuta*, on the other hand, is known to collect and consume bone from prey and abandoned carcasses (Hill 1989). Microwear studies on the carnassial of both of these species (*C. crocuta* and *P. leo*) further support the amount of bone

they are thought to consume (Schubert et al. 2010). *Panthera pardus* is also known to consume bone, in many cases entire carcasses (Brain 1981). Therefore similarities in carnassial robustness likely reflect the amount of bone typically consumed, rather than phylogenetic proximity. An additional significant dental character was the ratio between the length of the I3 and I2. An enlargement of the third incisor may represent an increased use of the incisors for gripping. A similar proposal has been made for *Homotherium latidens* (Anton et al. 2004A) and *Machairodus aphanistus* (Anton et al. 2004B); however, the incisors of *H. latidens* and *M. aphanistus* are also procumbent. While some species variability did occur here in this ratio, it seems to possess a lot of individual variation. It is likely that the I3/I2 ratio simply distinguished *Metailurus* from the modern felids, as its ratio was much higher than the others.

Remaining characters all relate to the basiocranium and the auditory bullae. The angle between the hypoglossal foramen and the jugular foramen was determined significant. Movement and feeling in the tongue are controlled by the hypoglossal nerve, which is located in the hypoglossal foramen (Reighard and Jennings 1901). The jugular foramen contains the internal jugular vein, the vagus nerve, the glossopharyngeus nerve, and several accessory nerves (Reighard and Jennings 1901). Because each of these foramina contains several veins and nerves, the angles between them could represent the amount of space necessary for each vein/nerve to exit the foramen. A greater angle may signify a greater availability of space for veins and nerves. *Panthera atrox* had the widest angle, suggesting this species had a well developed jugular vein and nerve complex. A similar conclusion can be made for the ratio between the hypoglossal diameter and skull length. Tongue control emerges from the hypoglossal foramen, therefore, a larger opening may allow for more nerves to exit. Because the tongue is often pulled back during the flehmen response (curling of the upper lip), it is possible

that greater movement and sensitivity in the tongue allows for greater reception of chemicals by the Jacobson's organ (Turner and Anton 1997). *Panthera onca* and *P. pardus* had the highest ratios, both of which are solitary and may rely on this reception when marking and exploring territories (Guggisberg 1975; Seymour 1989; Turner and Anton 1997).

Three muscles articulate to the mastoid process: the brachiocephalicus, sternocephalicus, and obliquus capitis anterior muscles, and together they are responsible for head depression and lateral rotation (Salesa et al. 2005). Opening of the mandible is controlled by the digastricus muscle, which articulates to the paroccipital process (Salesa et al. 2005). A greater distance between the paroccipital and mastoid processes may suggest an increased strength in head flexion or an increased gape (Salesa et al. 2005). Paroccipital to occipital condyle angle may reflect the shape of the atlas. A wider angle could indicate a greater distance between the articulating surfaces on the atlas, which would allow for a larger obliquus capitis anterior muscle. This would provide greater strength in head flexion and lateral rotation (Salesa et al. 2005). The final basiocranial character is the angle of the auditory bullae. It is apparent in feliforms that the angle of the auditory bullae controls the angle at which the auditory meatus is positioned. Wider angles appear to place the auditory meatus so it opens into the postglenoid process, while a shallower angle leaves the meatus unobstructed. Because the auditory meatus connects to the external ear, it is possible that this position reflects differences in how the ear is positioned and registers sounds. *Panthera tigris*, which has been observed to rely more on hearing than smell when hunting, had the widest angle (Nowak 1999).

### Phylogeny of Panthera

Within each phylogenetic tree, despite the outgroup, there were noticeable consistent patterns. For example, *Panthera atrox* is frequently placed as a sister taxon to *P. leo*. When these pairings occur, *P. tigris* is frequently placed as the sister taxon to that pair. In some cases however, *P. atrox* was paired with *P. tigris*. This consistent relationship between these three species suggests the similarity of several characters and may indicate a strong phylogenetic relationship between the three. Based on this consistency, it seems likely that *P. atrox* has a lion or tiger ancestry or that the three species recently diverged from a common ancestor. When *Pseudaelurus validus* is used as the outgroup, *Panthera atrox* pairs with *P. leo* as well as *P. onca*, *P. pardus*, or is basal to *P. onca* and *P. pardus*. This relationship to *P. onca* and *P. pardus* may be true due to *Pseudaelurus* often being considered the first taxon to possess a truly felid body plan, while the other outgroups may be too basal or derived (in the case of *Crocota*) to accurately reflect the phylogeny of *Panthera*. However, it must also be taken into consideration that for each outgroup, with the exception of *C. crocuta*, PAUP was unable resolve the relationships between the species of *Panthera* and placed them all at the same node on a consensus tree. A majority of the trees produced, despite the outgroup, consistently placed *N. nebulosa* and *U. uncia* outside the *Panthera* clade. This supports previous studies that have classified these species as pantherines (e.g. Johnson and O'Brien 1997), instead of within *Panthera*.

When the relationships obtained here are compared to previous genetic studies, it becomes apparent that the morphology of these felids does to an extent reflect the genetic phylogenies. Johnson and O'Brien (1997) found a sister taxa relationship between *P. leo* and *P. tigris*, while Yu and Zhang (2005) concluded that *P. tigris* instead was more basal than *P. leo*.

Both conclusions were supported here depending on the outgroup chosen. Because *P. atrox* is included here, and not in molecular studies including all of *Panthera*, a direct comparison of accuracy cannot be made between the relationships; however, the results here do support a close phylogenetic relationship between *P. leo* and *P. tigris*. In all of the molecular studies discussed here, *N. nebulosa* is basal to the other pantherine species. Such a relationship is also consistent with the phylogenies obtained with each outgroup here, suggesting that a basal relationship to *Panthera* is supported by both molecular and morphological data and likely represents a true relationship. *Uncia uncia*, however, appears to be a basal species here but is consistently seen as highly derived in the molecular studies (Yu and Zhang 2005; Davis et al. 2010). Differences in phylogenetic placement could suggest that the snow leopard retains more basal felid characters, despite being a “younger” species. It is also possible *U. uncia* appears less derived here because the characters chosen do not reflect the derived characters of *U. uncia*. Relationships between *P. onca* and *P. pardus* vary depending on the previous study in question; however, one is typically a sister taxon to the other, which also occurs here.

Other morphological studies place both *U. uncia* and *N. nebulosa* as basal to *Panthera*. This relationship to *Panthera* is consistent with the findings here; however, their relationship to one another differs depending on the analysis. Christiansen (2008A) found that the clouded leopard was more basal than the snow leopard, while Salles (1992) concluded the opposite. Here, both relationships were present; however, the clouded leopard was only more basal when *Pseudaelurus validus* was the outgroup. Christiansen (2008A) and Salles (1992) concluded that *Panthera tigris* was the most basal species in *Panthera*. Such a relationship was not found here and instead *P. tigris* was often one of the most derived species. Christiansen (2008A) and Salles (1992) also found that *P. leo* and *P. onca* share a common ancestor. Salles (1992) was unable to

resolve the relationships among *P. leo*, *P. onca*, and *P. pardus*, suggesting this relationship may or may not be real. None of the trees created here support such a relationship. Christiansen (2008) concluded that *P. atrox* shared a common ancestor with the jaguar and was more basal than *P. leo*. With the exception of the analysis using *Pseudaelurus validus* as the outgroup, no such relationship was supported here. Instead, *Panthera atrox* consistently paired with *P. leo* or *P. tigris*. It must be noted, however, that with the exception of *Crocuta crocuta*, each phylogenetic analysis was unable to resolve the phylogeny within *Panthera* in a consensus tree.

Holliday and Steppan (2004) found that species that have reached hypercarnivory, such as felids, exhibit much less morphological diversity between each other than other carnivores, such as mustelids. Because of this loss of morphological variation, it is very difficult to identify apomorphies within felids (Holliday and Steppan 2004). This is apparent by the inability of many of the phylogenetic trees to discern the evolutionary relationships within *Panthera*. For example, Wroe and Milne (2007) found, within their analysis of carnivore skull shape, that all modern *Panthera* plot within the same morphospace. Specifically, *P. leo*, *P. tigris*, *P. onca*, and *P. pardus* all have wide skulls at the zygomatic arch, deep nasal region, and a relatively short rostrum. Because each of these cats hunt prey typically larger than themselves, it suggests that skull shape could be a reflection of hunting styles (Wroe and Milne 2007). It is interesting to note, however, that *P. atrox* did not plot in the same morphospace as the other pantherines. Instead *P. atrox* plots with a short rostrum but a narrower skull and shallower nasal region. This difference in skull shape could reflect a difference in hunting styles or prey size/type for *P. atrox*. Moreover, it seems unlikely that this difference is a reflection of phylogeny because *P. atrox* consistently plots within *Panthera* in phylogenetic analyses (including this study) and the other pantherines plot together in Wroe and Milne's (2007) study. Christiansen (2008B) also found

that all members of *Panthera* occupy the same skull shape morphospace. However, the inclusion of saber-toothed felids in that study resulted in a great amount of overlap between felids, suggesting that there could be greater differences present between species that was not reflected in the analysis (Christiansen 2008B). Removal of the saber-toothed felids, which are considerably different from modern felids, may resolve the relationships within modern felids. Overall, it is apparent that the shift toward hypercarnivory in felids has caused a great deal of convergence in skull morphology, making a true phylogeny very difficult to create through morphological means.

The goal here was to approach pantherine phylogeny through characters that were unaffected by morphological convergence associated with hypercarnivory. Consequently, character selection focused on the basicranium and included the auditory bullae, surrounding foramina, and processes. Previous studies have concluded that the auditory region in mammals is significant in phylogeny (Hough 1944; Hough 1952; Novacek 1977; Ivanoff 2001). Each of these studies included the internal structure of the auditory bulla. Here, the internal structure could not be included due to the damage it would cause on the modern and fossil skulls. Because only the external structure of the bulla was included, only a portion of the phylogenetic information could be obtained. Future inclusion of internal structures (perhaps via CT scanning) could help better resolve the relationships within *Panthera*. Current understanding of the function of bullae structures makes it difficult to draw conclusions regarding the significance of differences between species (Novacek 1977). It is, therefore, important for future analyses to not only address differences in the auditory bullae between species but also the purpose of these differences to gain a better understanding of felid phylogeny.

## CHAPTER 5

### CONCLUSIONS

By choosing four different outgroups, more confidence can be bestowed on the phylogenetic relationships created than can be said from a single outgroup. Based on the morphological characters used here, a relationship between *Panthera leo* and *P. atrox* is supported, whereas one between *P. onca* and *P. atrox* is not. However, the relationship between *P. leo* and *P. atrox* is not consistent enough to suggest the two species are synonymous. Instead, based on my analysis, I suggest the two are likely sister taxa and that they share a common ancestor. Inclusion of the European cave lion, *P. spelaea*, may provide more insight on the relationship between the “lions”. Retention of the name *Panthera atrox* and not previous names such as *P. leo atrox* is supported here. In addition, the consistent basal position for *Uncia uncia* supports that the species should not be included in the genus *Panthera*. Molecular phylogenies using *C. crocuta* as the outgroup compare well with the morphological phylogeny created here. This suggests that despite the spotted hyena being a highly derived species, its characters make it an appropriate outgroup to *Panthera*.



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## APPENDICES

### Appendix A- Specimens analyzed

*Crocota crocuta* NMNH 182095, 182101, 182103, 15202, 182105, 182082, 182084, 182085, 182091, 182032, 182110, 182117, 182114; AMNH 187769, 52064, 187773, 52065, 52060, 83593, 187777, 80621, 81833, 52063, 52059, 187775, 187771, 83592

*Panthera leo* NMNH 163328, 163329, 163330, 161920, 176201, 12250, 182107, 181571, 181572, 181573, 181574, 181575, 181576, 589605, 181578, 181579, 181581, 182143, 181580, 181582, 181583, 181584, 181585, 181586, 181587, 181588, 181589, 181590, 162913, 162914, 162915, 162916, 162917, 162919, 155439, 161914, 161915, 161916, 161917, 161923, 61753, A8548, 20860, 20859, 565762, 181577, 271321, 268924, 161921, 162918, 161913, 174743, 174744, 174742, 182313, 163109, 182339, 182315, 182297, 182324, 182325, 182326, 182308, 182309, 182311, 182332, 182296, 182333, 182293, 182294, 182295, 182423, 182420, 182421, 161919, 181569, 163108, 182044, 181592, 197137, 105401, 199707, 199524, 172677, A22705, 153525, 125344, 197944, A12319, 254455, 367397, 256196, 236920, 216601, 216602, 216604, 216603, 181930, 184816, 537000, 155443, 155442, 174639, 539997, 539998, 539999, 63362, 282303; AMNH 54995, 83617, 83618, 81837, 52072, 52077, 54996, 52075, 52076, 52074, 52073, 169463, 81843, 81844, 30242, 30247

*Panthera tigris* NMNH 396137, 123444, 396272, A8549, 304513, 399096, 583694, 583778, 278470, 536099, 399298, 152192, 152193, 152194, 258210, 15525, 141898, A49773, 14984, 62074, 62075, 174981, 251789, 269320, 536895, 239445, 239450, 16099, 16100, 61329, 61330, 61331, 61332, A49728, A49797, A49799, A49798, 270988, 270989, 361847, 395855, 253291, 253292, 253293, 253294, 253295, 253296, 253297, 271556, 253285, 111982, 253288, 218321, 253286, 253287, 253289, 253290, 143191, 188638, A3804, 254713, A16144, A16145, 396654, 254977, 588759, 399556, 220265, 221016, 582442, 395727, 49740; AMNH 54460, 22334, 54459, 54458, 113744, 100024, 113743, 87348, 90016, 119680

*Panthera onca* NMNH 269786, 125353, 589080, 141897, 122602, 125453, 155615, 155603, 259038, 125349, A25097, 557719, 464972, 583256, 231961, 225613, 244507, 289015, 247337, 294541, A8003, 12176, 61192, 238669, 336224, A14177, 338356, 338357, 338358, A36283, 140949, 239343, 281420, 281421, 131498, 131499, 167894, 251118, 251119, 105930, 181231, 244858, 287497, 287498, 287499, 249822, 249823, 249824, 249825, 249826, 179170, 179171, 249821, 130362, 132519, 132755, 134500, 134501, 147362, 127542, 9390, A 13845, 131998, 88044, A6480, A9703, A9704, A13846, 256376, 256377, A49393, 100122, 137039, 270363, 361043, 374849, 339678, 443722, 456774, 388248, 256385, 256386, 256388, 362249, 362250, 395084, 395085, 256387, 256389, A12296, 236368, A4362, 100123, A4128, A4361, 123527, 268871, 67403, 100541; AMNH 146987, 36229, 11084, 25011, 98682, 147513, 98841, 147510,



11085, 11083; UF 12143, 12158, 12161, 12159, 12160, 12164, 12155, 12156, 12149, 12151, 12145

*Panthera pardus* NMNH 145261, 252904, A14401, 236969, 13357, 344212, 270896, 164763, 182178, 303320, 164764, 254536, 254537, 254637, 173328, 173329, 256125, 258857, 318981, 199061, 171879, 164555, 164557, 21654, 259410, 258177, 256668, 256099, 175743, 172662, 162926, A16143, 161911, 182338, 182318, 182323, 163093, 182328, 182329, 182331, 163095, 164544, 164545, 181595, 163094, 162927, 396007, 290875, 261367, 241556, 282239, 258660, 276996, 364963, 102583, 201568, 270126, 155613, A21350, 181600, 257396, 155403, 15230, 239866, 271289, 329353, 329352, 396948, 292310, 543375, 296141, 296142, A22643, 156284, 589634, 14312, 254445, 14337, 557720, 216607, 253298, 13067, 240485, 162147, 216606, 256130, 173330, 173331, A34866, 236921, 239610, 184818, 162144, 162145, 162146, 184819, 522719, 144977, 13047; AMNH 170296, 186944, 52023, 57008, 52044, 89010, 170290, 170291, 170310, 170307, 52010, 52008, 80174, 189390, 189391, 52042, 34111, 87236, 34745, 88628, 88627, 161733

*Neofelis nebulosa* NMNH 319205, 545387, 589133, 282124, 399290, 399291, 580716, 581891, 396639, 198705, A49974, 575150, 172673, 172674

*Uncia uncia* NMNH 84091, 307383, 337500, 321948, 252543, 241212, 557721, 176048, 307649, 589696; AMNH 42822

*Panthera atrox* LACMHC 2900-6, 2901-6, 6992, 6984, 6994, 17489, 6988, 6991, 6993, 587, 2900-15, 2901-15, 6990, 585, 2901-26, 2900-16, 286/586, 2901-5, 2900-15, A3431, 2900-10, 2900-12, 17527, 2900-17, 2900-18, 2900-19, 2900-8, 2900-20, 2900-7, 2901-7, 2900-5, 2901-5, A3431, 10164, 17149, 17524, 17526, 6974, 2900-14, 6972, 17518, 17519, 6970, 6971, 2900-1, A3429, A3432, A3430, A3428, 6977, 6967, 6969, 17521, 6978, 6968, 17502, 60187, A3407, 60189, 2900-3, 52033, 21078, 15678, 15404, 2900-9; UF 9076; AMNH 9076, 30460, 30754, 69028, 69031, 69026, 30751, 30752, 14310, 69048, 69047, 30759, 69013, 30760, 11069, 69002, 69473, 69016, 30757

*Metailurus* ssp. AMNH IVPP 45- L399 (cast), 95294, 131854; PMU M3841, M3835

*Proailurus lemanensis* AMNH 101931

*Pseudaelurus validus* AMNH 61834, 61827, 61828

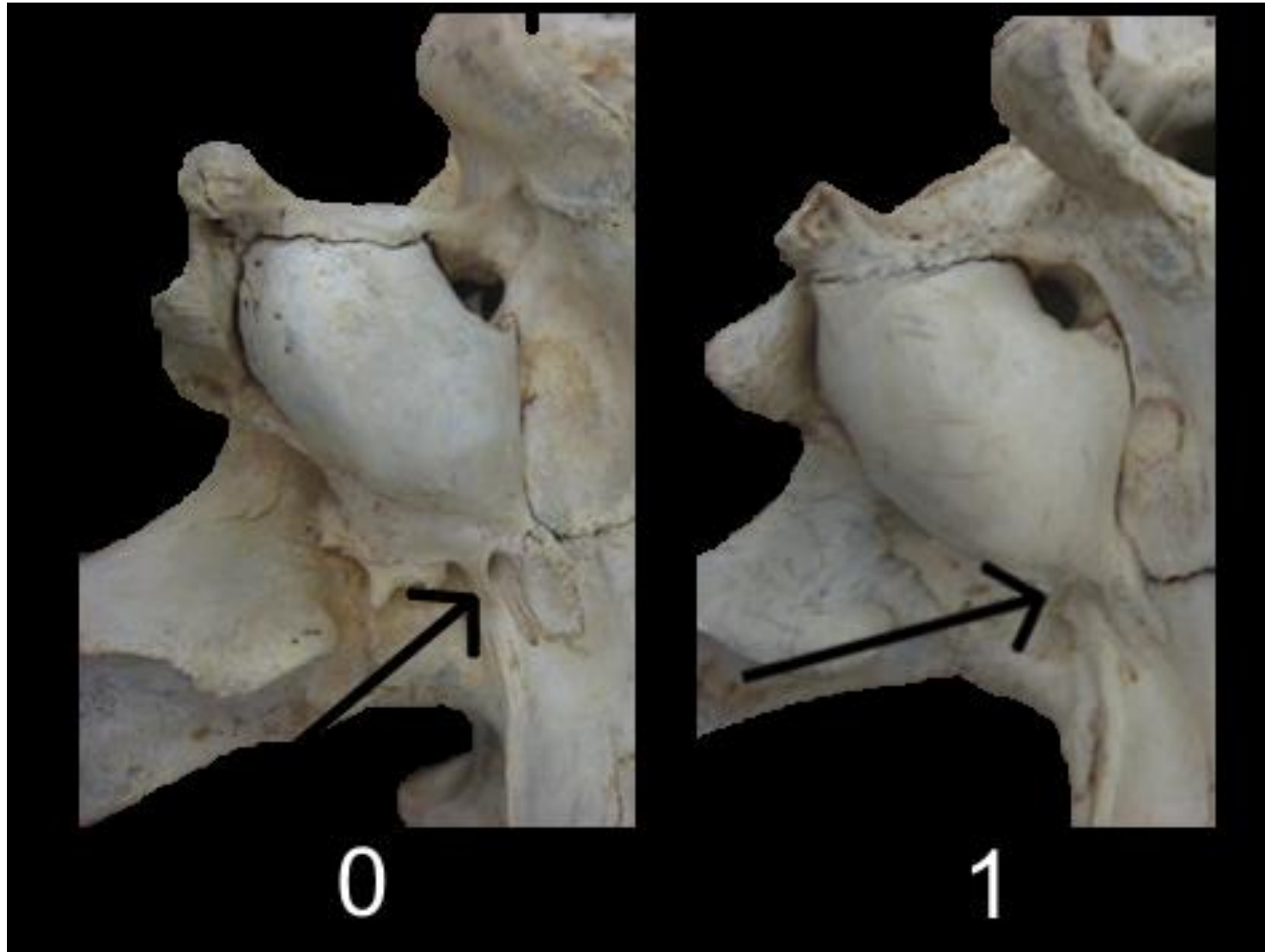
Appendix B- Character descriptions using *Crocota crocuta* as the outgroup

Dental terminology from Hershkovitz (1971) and Salles (1992); Characters 12 and 13 modified from Christiansen and Harris (2009); Character 15 modified from Christiansen (2008); Characters 21 and 22 from Merriam and Stock (1932); Characters 3, 25, 26, and 27 from Salles (1992)

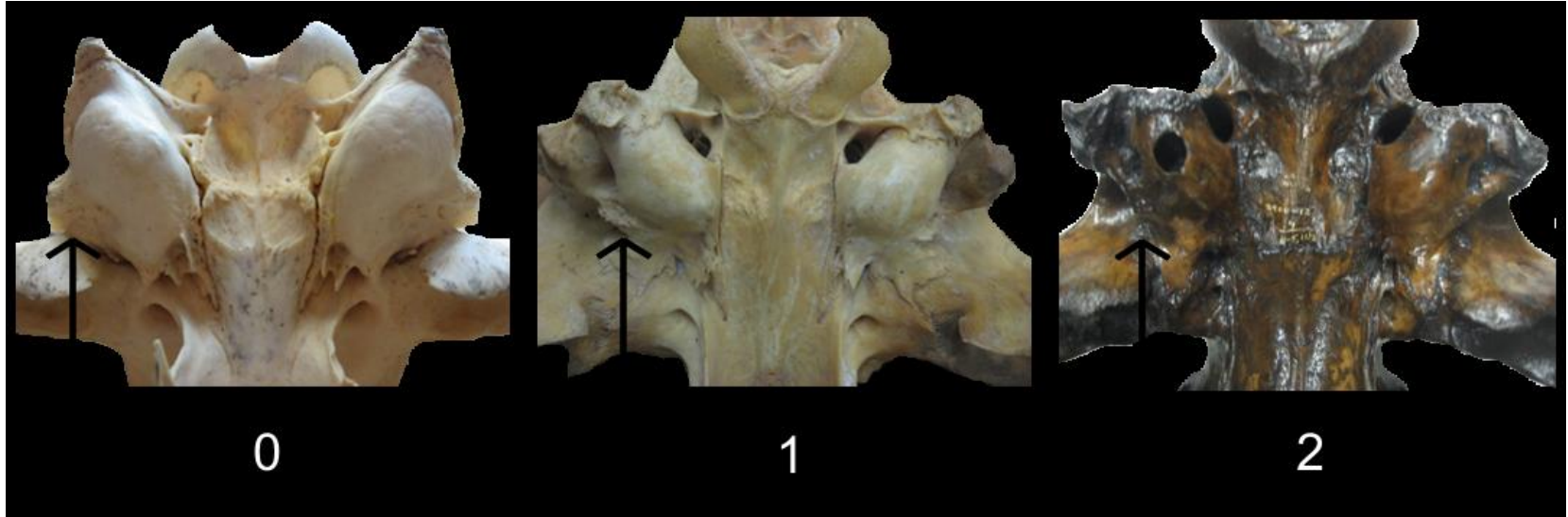
1. Angle of auditory bulla spans between  $22^{\circ}$  and  $47^{\circ}$  (0) or is restricted between  $32^{\circ}$ - $47^{\circ}$  (1). This angle was measured by creating a straight line between the center of the occipital condyles and premaxilla and another straight line from the center of the paroccipital process to the anterior-most point on the bulla. The angle measured was between the intersection of these two lines.



2. Process between entotympanic and ectotympanic (above vidian nerve canal) does not (0) or does protrude ventrally (1).

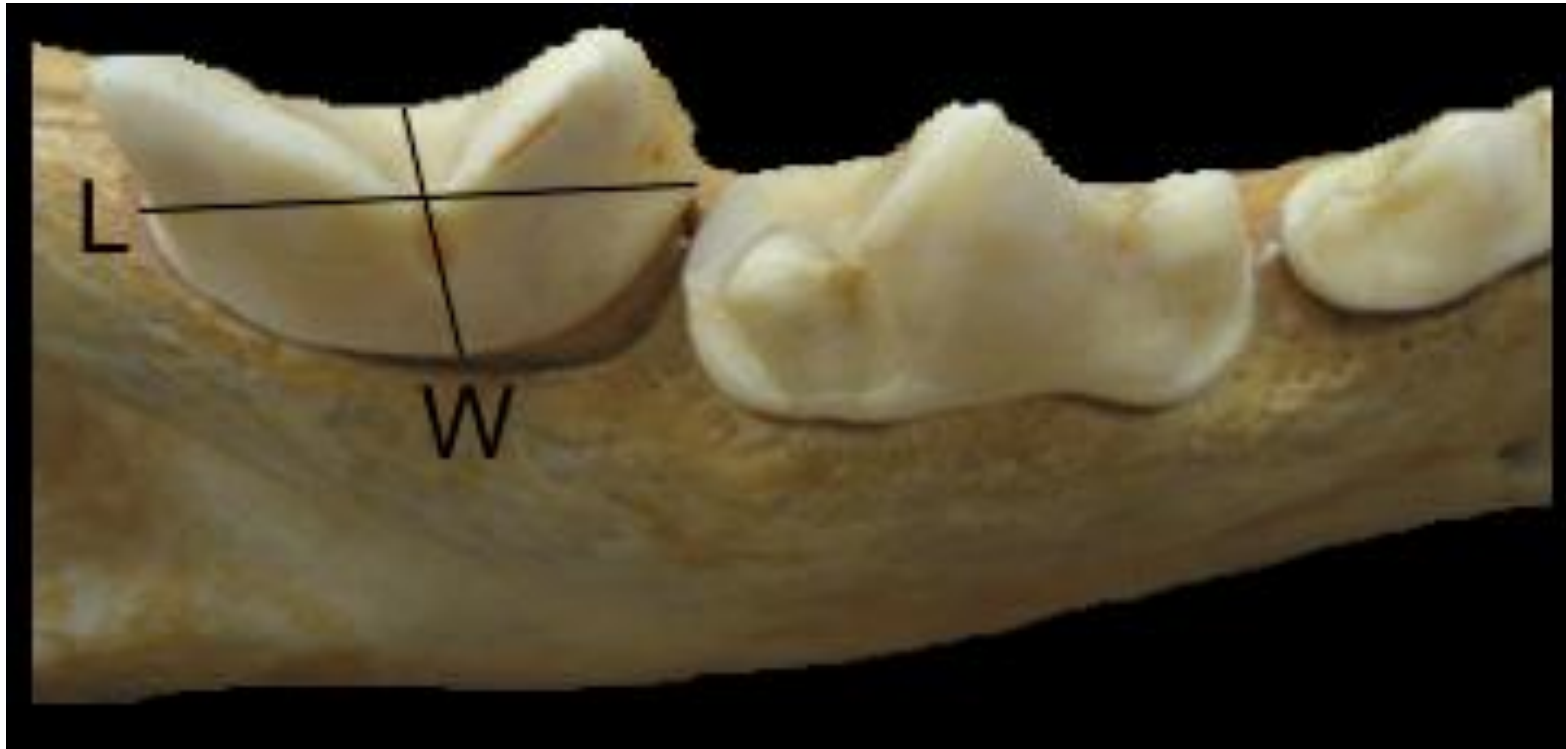


3. Auditory meatus consists of a complete tube (0), a small projection (1), or is entirely absent (2).

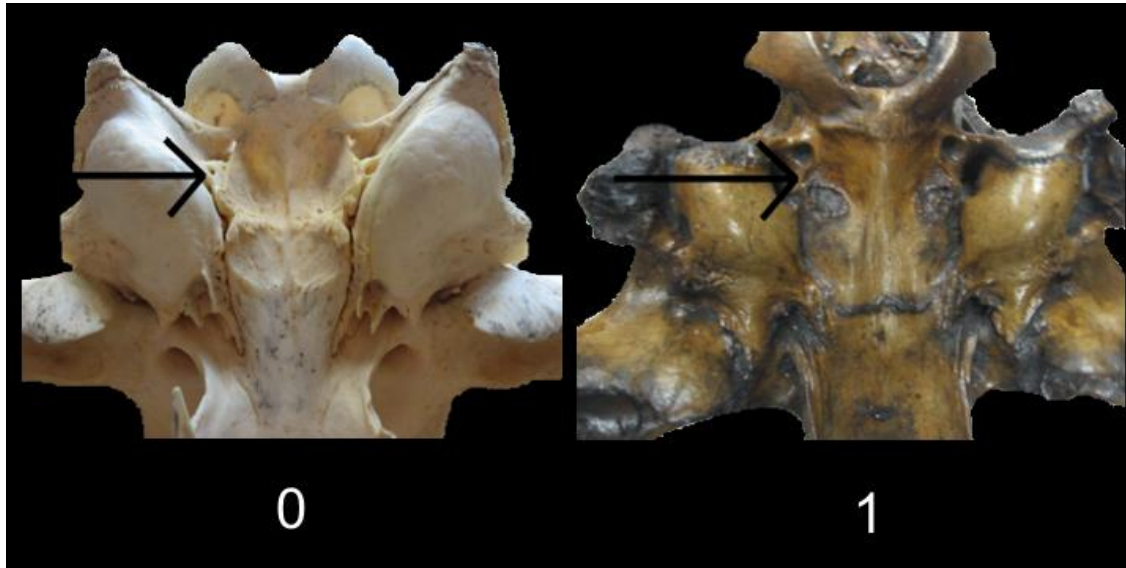


4. M1 is absent (0) or present (1)

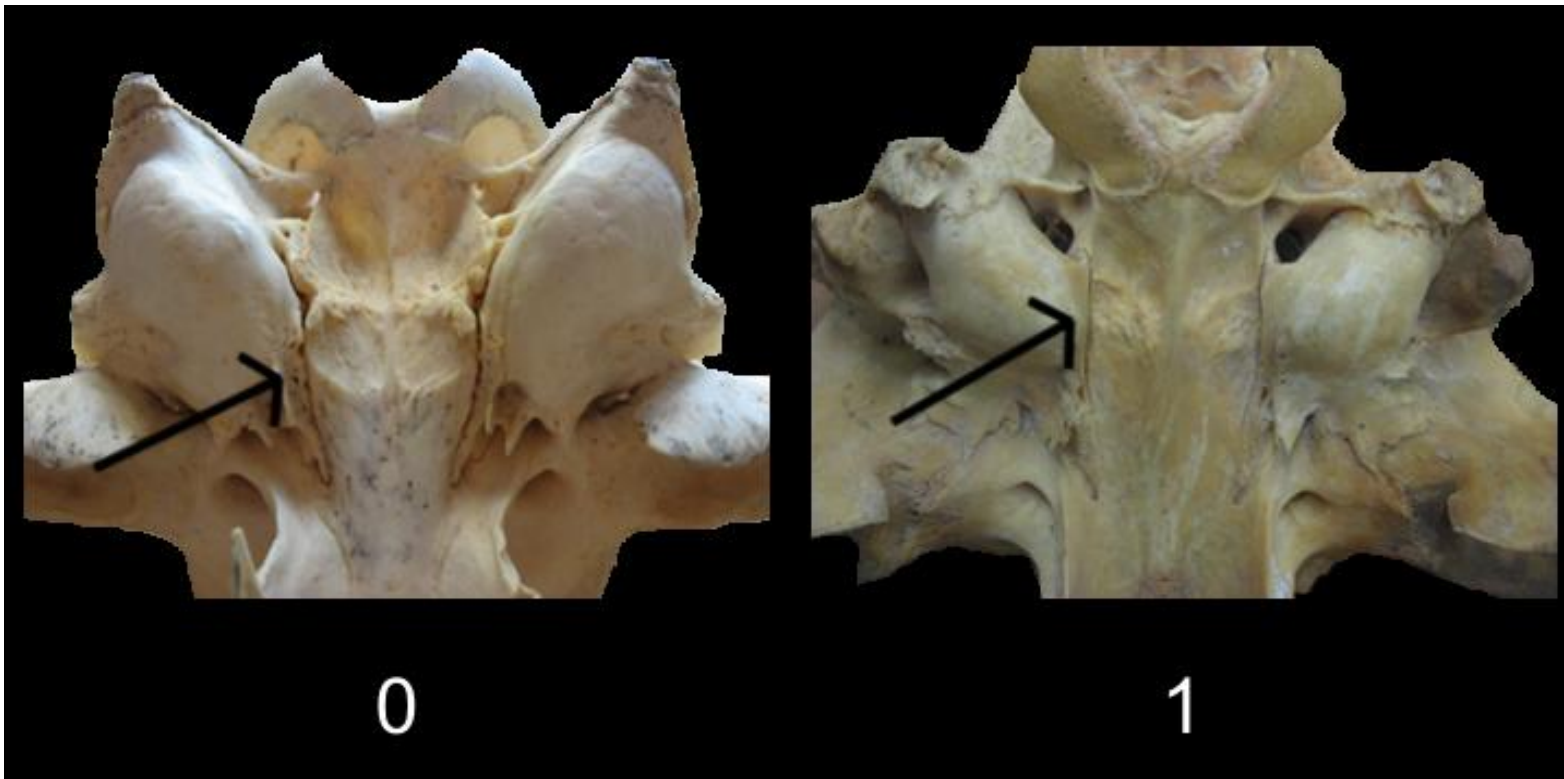
5. Ratio of M1 length to width greater than 2.25 (0), between 1.0-3.25 (1), or greater than 2.25 (2).



6. Protocone is wider than anterior parastyle (0) or is equal or thinner in width (1). Measurements were made using digital calipers at the widest anterior-posterior point of the cusps.
7. Occipital has depressions (0) or is flat (1).



8. Suture between occipital and auditory bulla visible ventrally (0) or not visible and tucks below bulla (1).



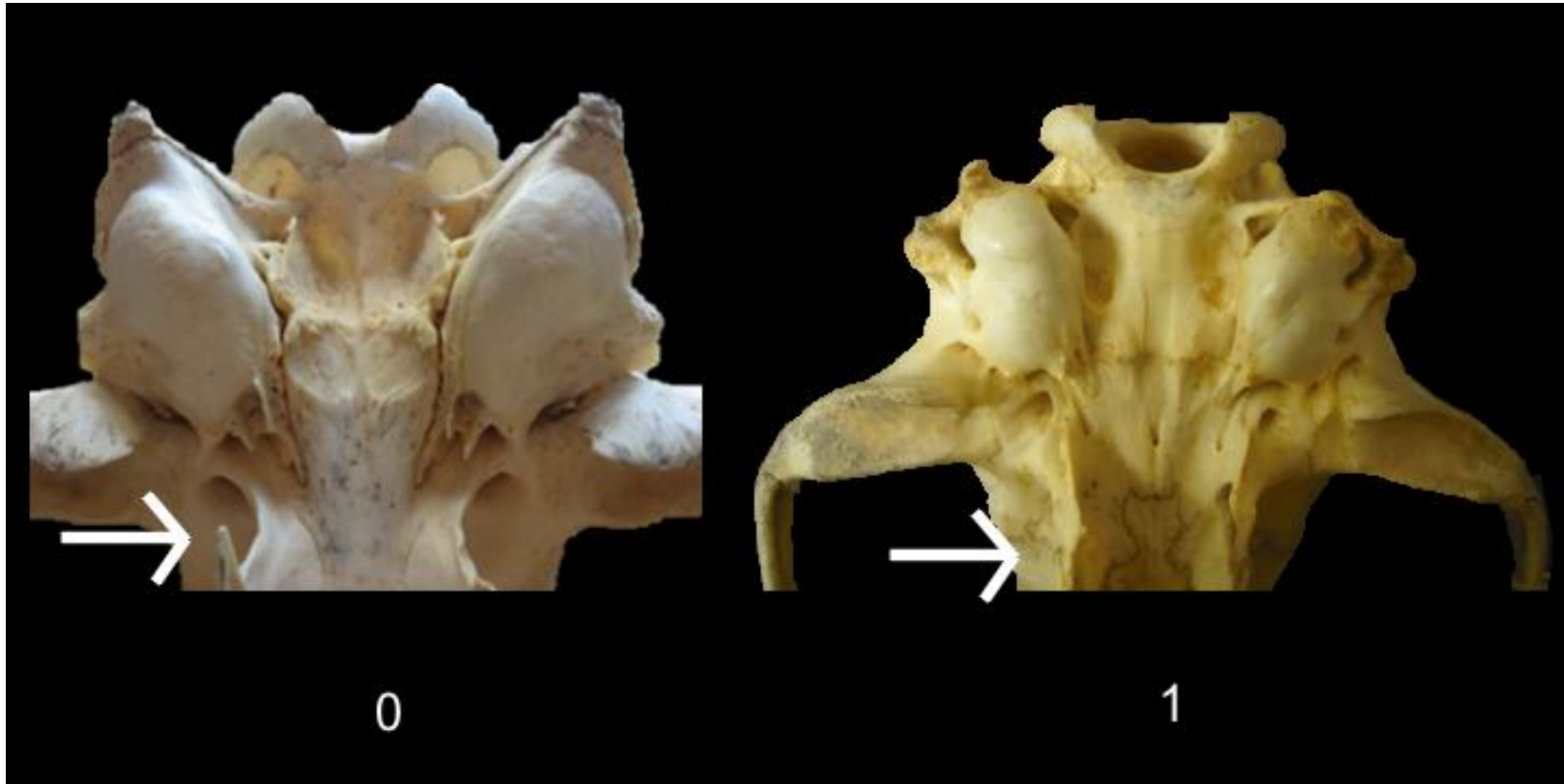


9. Lamboidal crest reduced (0) or well developed (1).





10. Superior orbital fissure not visible in ventral view (0) or is visible (1).



11. Foramen ovale intersects with the pterygoid process of the basisphenoid (0) or does not intersect (1).



12. Angle between the maxilla and postorbital process is less than  $90^\circ$  (0), is between  $85^\circ$ - $105^\circ$  (1), or is greater than  $90^\circ$  (2). This measurement was achieved by drawing a straight line along the maxillary tooth row from the P2 to M1 and then measuring the angle of the postorbital process to this line.



13. Frontal nasal suture is anterior to maxillary frontal suture (0), is level with the maxillary frontal suture (1), or is posterior to the maxillary frontal suture (2).



14. Infraorbital foramen is visible in lateral view (0) or is not visible (1).



15. Lacrimal process is absent (0) or present (1).



0



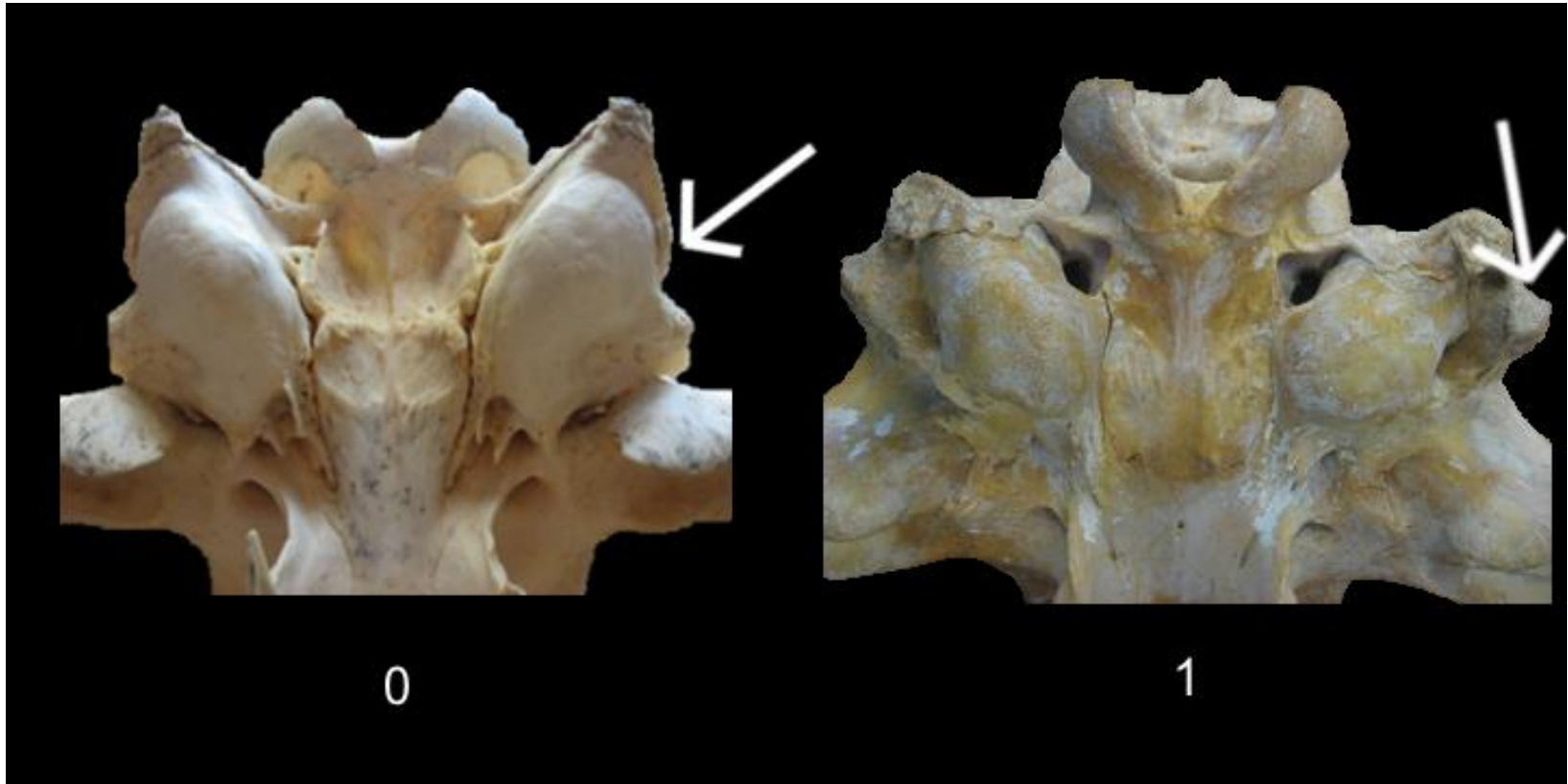
1

16. Foramen rotundum is not visible in lateral view (0) or is visible (1).



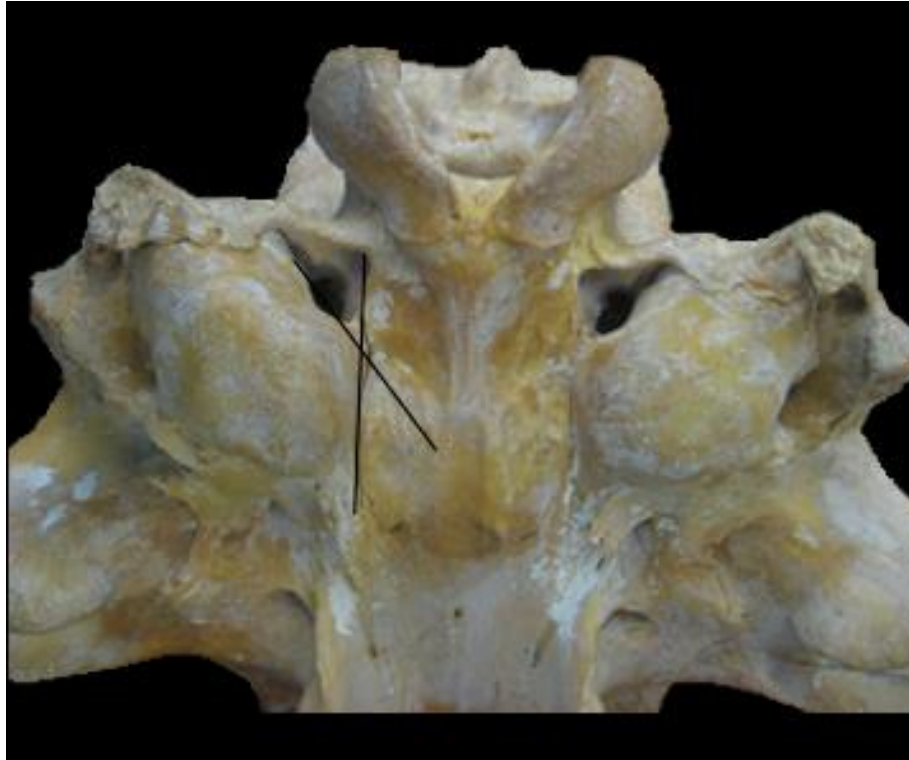


17. Mastoid process is reduced (0) or well developed (1).





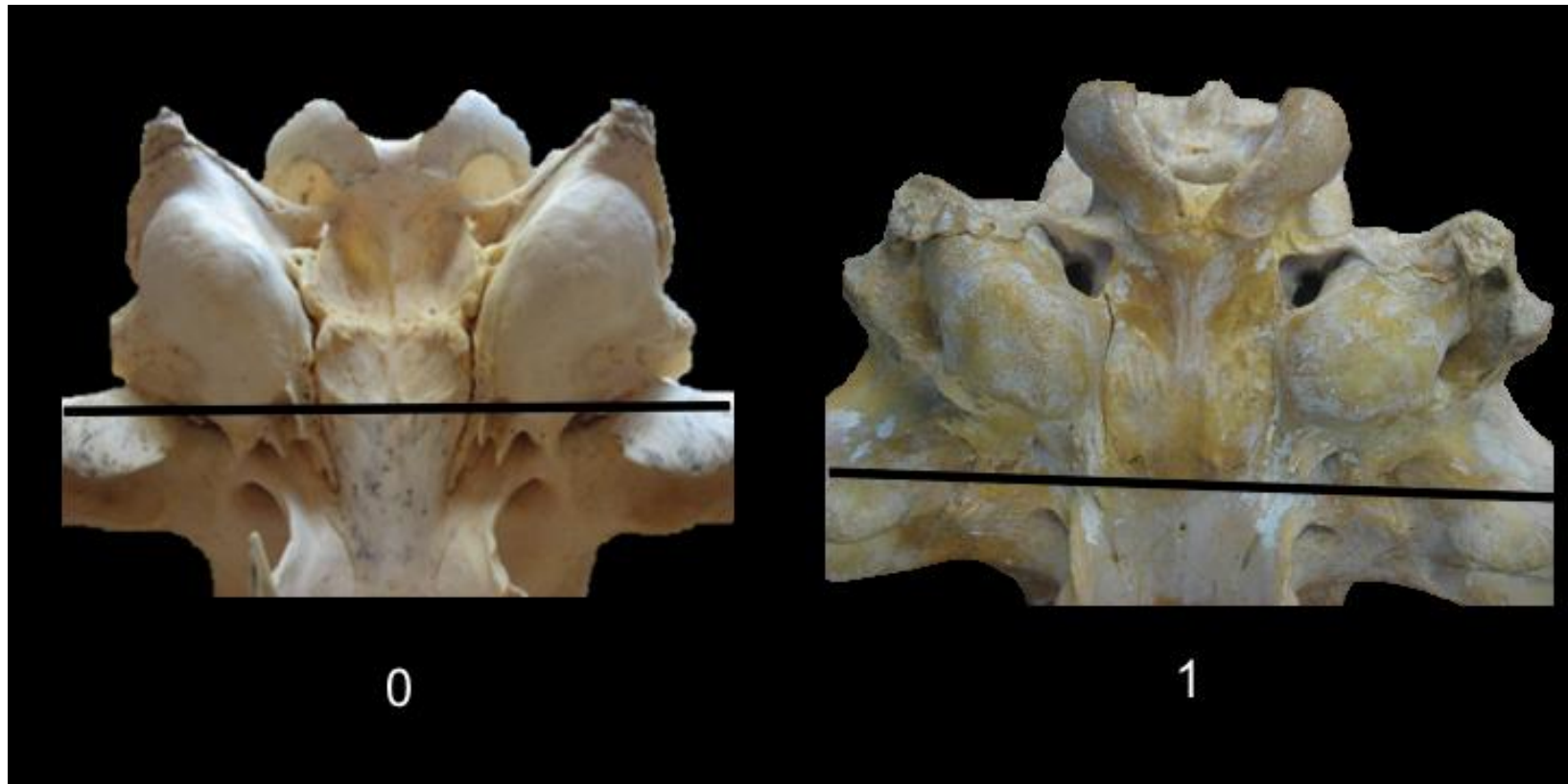
18. Angle between the hypoglossal and jugular foramina is less than  $40^\circ$  (0) or is between  $18^\circ$ - $55^\circ$  (1). This angle was measured by bisecting each foramen and measuring the angle at which both lines intersected.



19. Foramina are medial to the Vidian nerve canal (0) or absent (1).



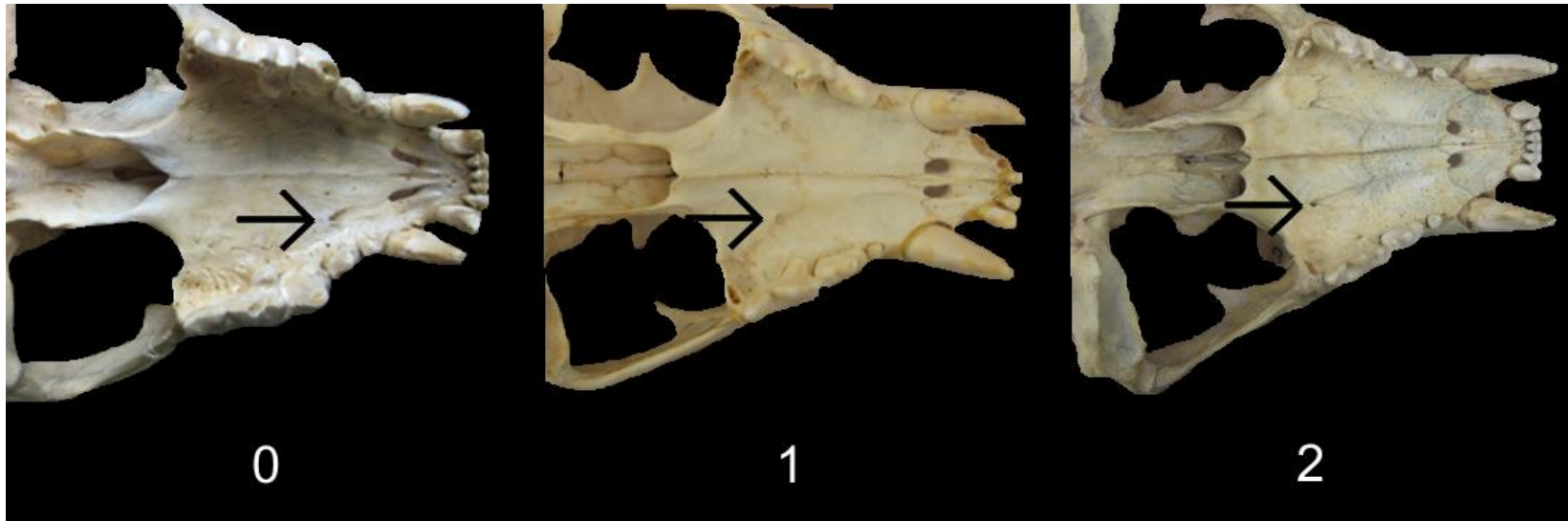
20. Auditory bullae intersect with the posterior-most point of the post glenoid process (0) or do not intersect (1).



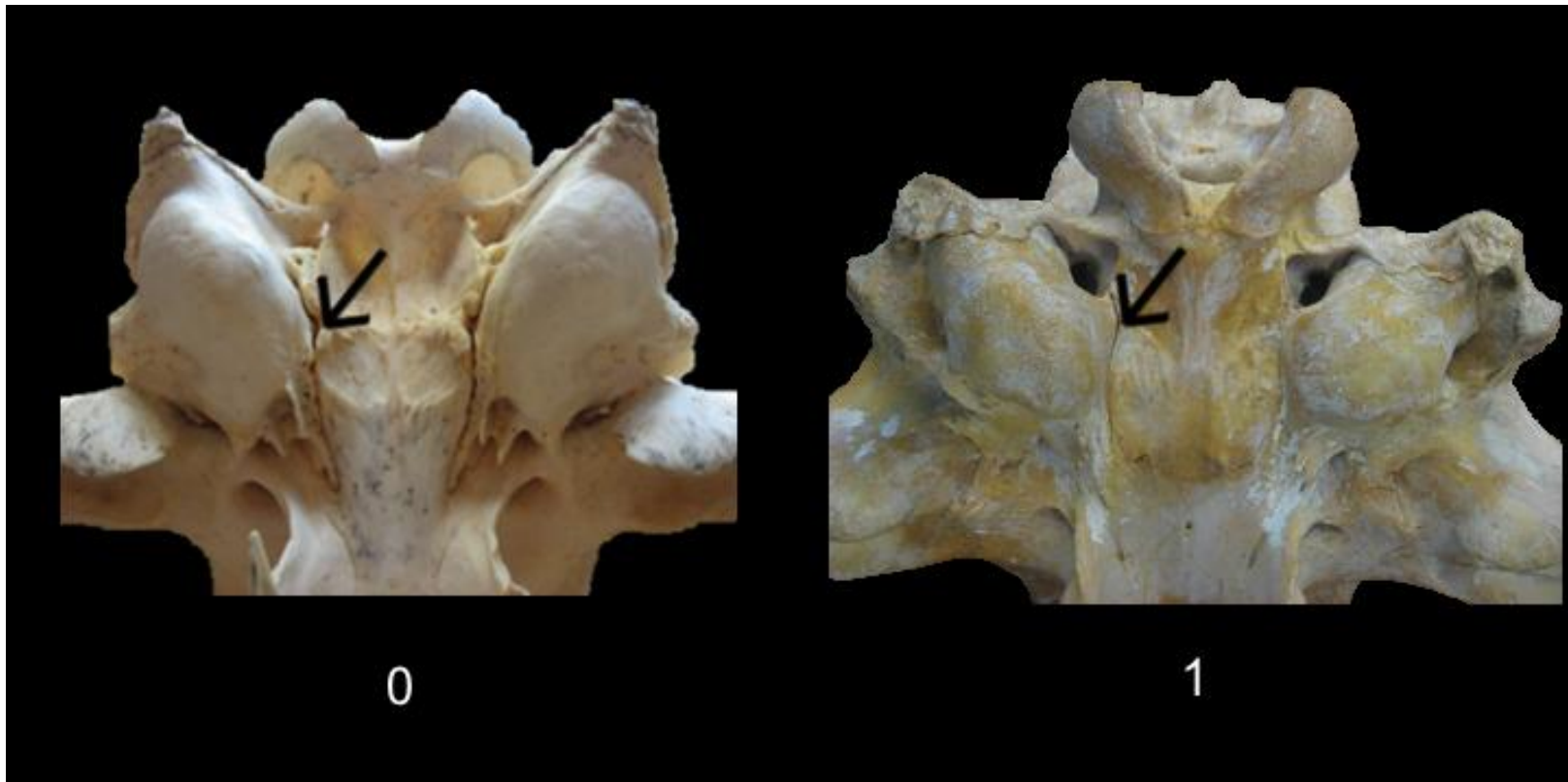
21. Ratio of distance between postorbital process and frontal parietal suture to skull length is greater than 0.2 (0), is between 0.18-0.3 (1), or is less than 0.2 (2). This measurement was made by extending a line perpendicular to the frontal parietal suture from the postorbital process and measuring the distance.



22. Posterior palatine foramen is anterior to the carnassials (P4) (0), is anterior to the carnassial notch but posterior to the carnassial (1), or is posterior to the carnassial notch (2).



23. Foramina are present along the auditory bulla occipital suture (0) or absent (1).

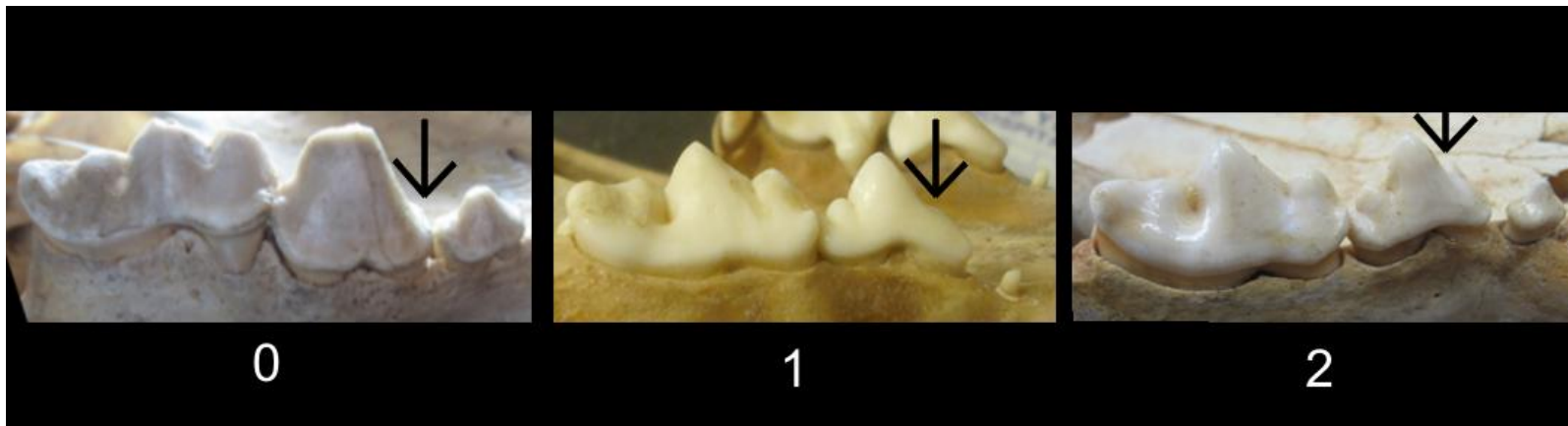




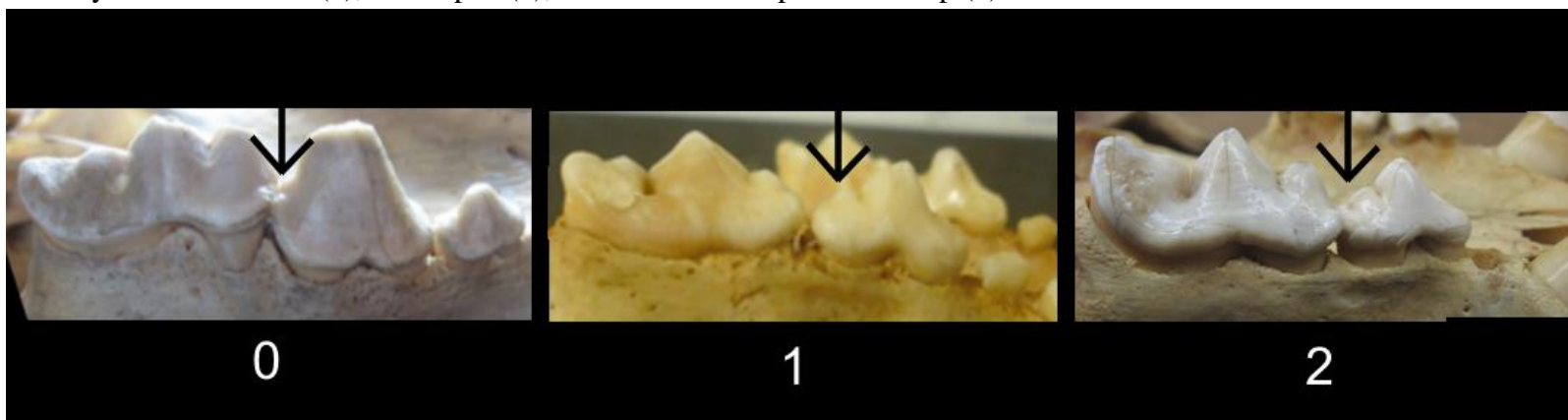
24. Infraorbital foramen is pinched and slit-like (0) or is an open oval (1).



25. Parastyle on P3 is absent (0), reduced (1), or well developed (2).



26. Metastyle reduced in P3 (0), developed (1), or has additional posterior cusp (2).





27. Ratio of upper canine length to skull length is less than 0.2 (0), is between .09-.26 (1), or is greater than 0.2 (2). Canine length was measured from where the canine entered the skull (end of root) to tip using digital calipers. Skull length was measured across the ventral view of the skull from the anterior-most point of the occipital condyle to the anterior-most region of the palate.

28. p2 is present (0) or absent (1)

29. P3 is enlarged to nearly the same size as P4 (0) or is reduced (1).



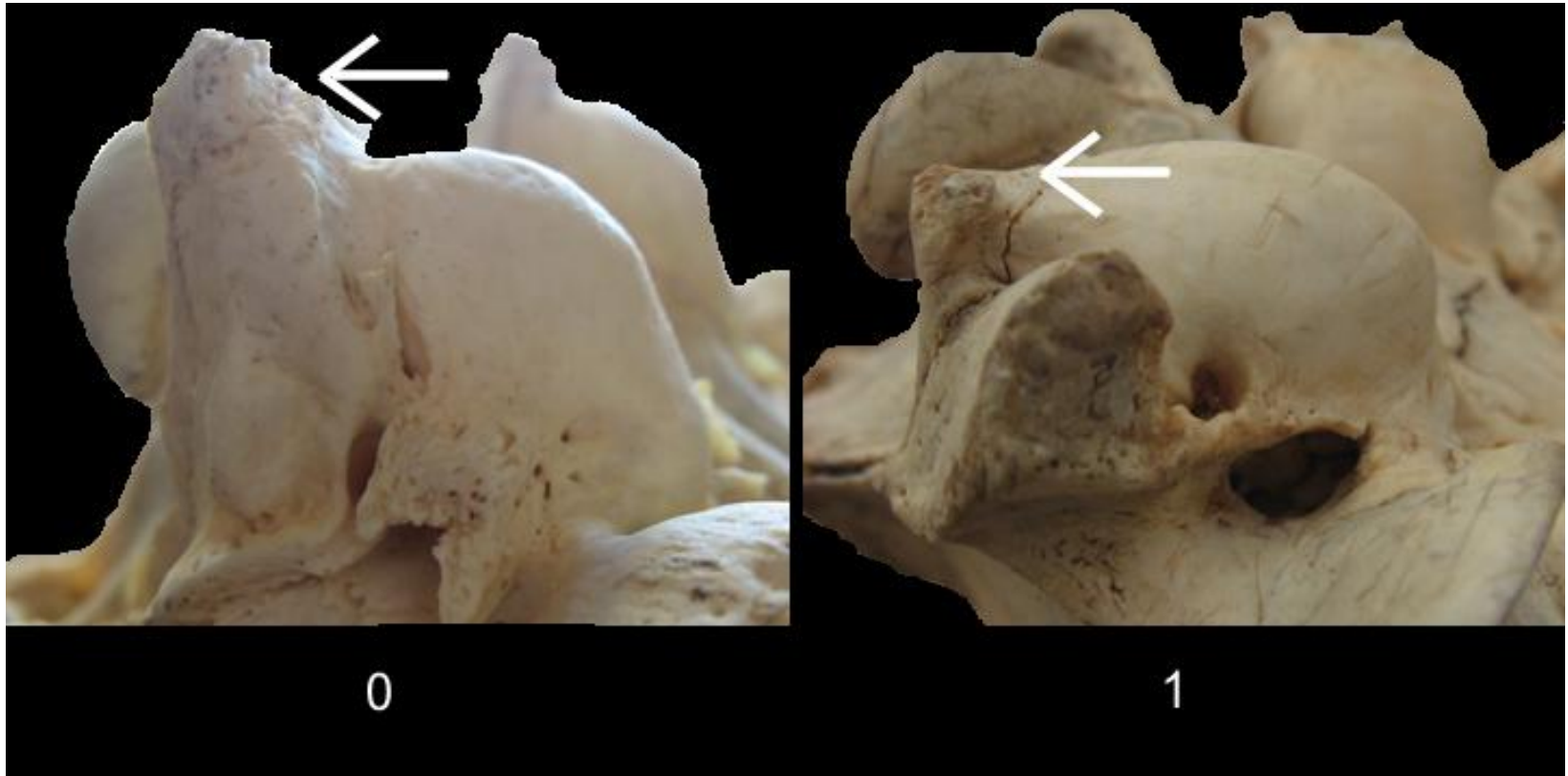
30. Paraconid on p3 is absent (0) or present (1).



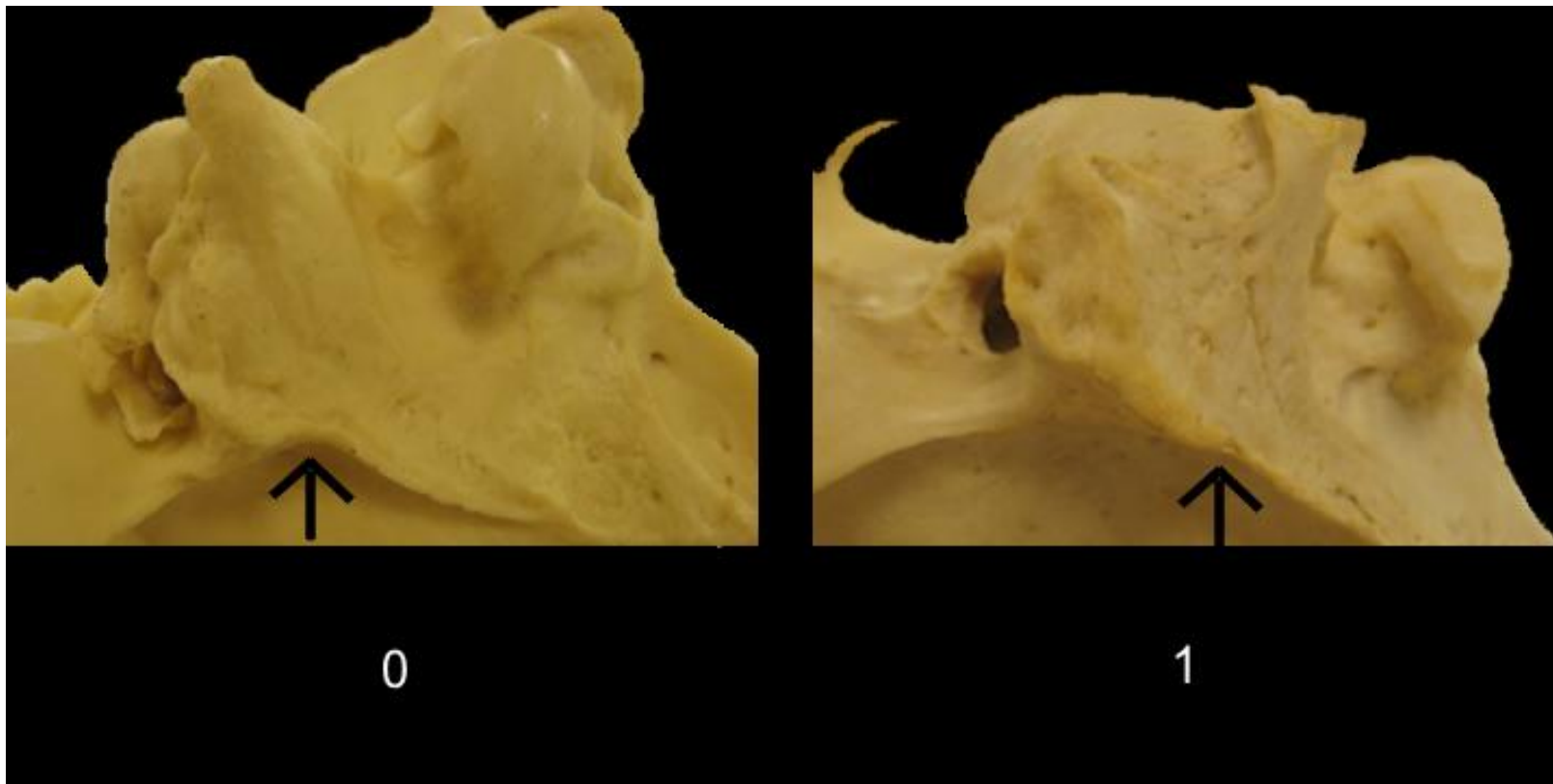
31. Paraconid on p4 is smaller than first posterior accessory cusp (0) or is the same size (1).



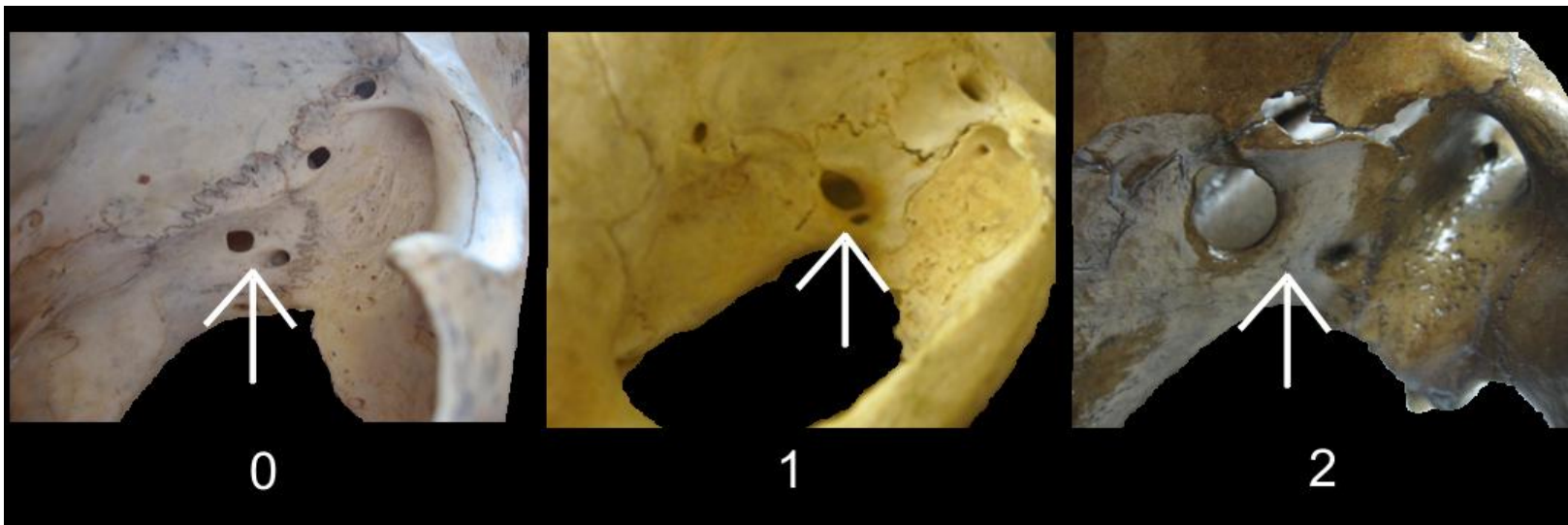
32. Paroccipital process extends ventrally beyond bullae height (0) or does not extend above bullae height (1).



33. Lateral side of mastoid process does not intersect with lambdoidal crest (0) or does intersect (1).



34. Foramina on lateral palatine spaced at medium distance (0), nearly overlap or have completely merged (1), or spaced very far apart (2).

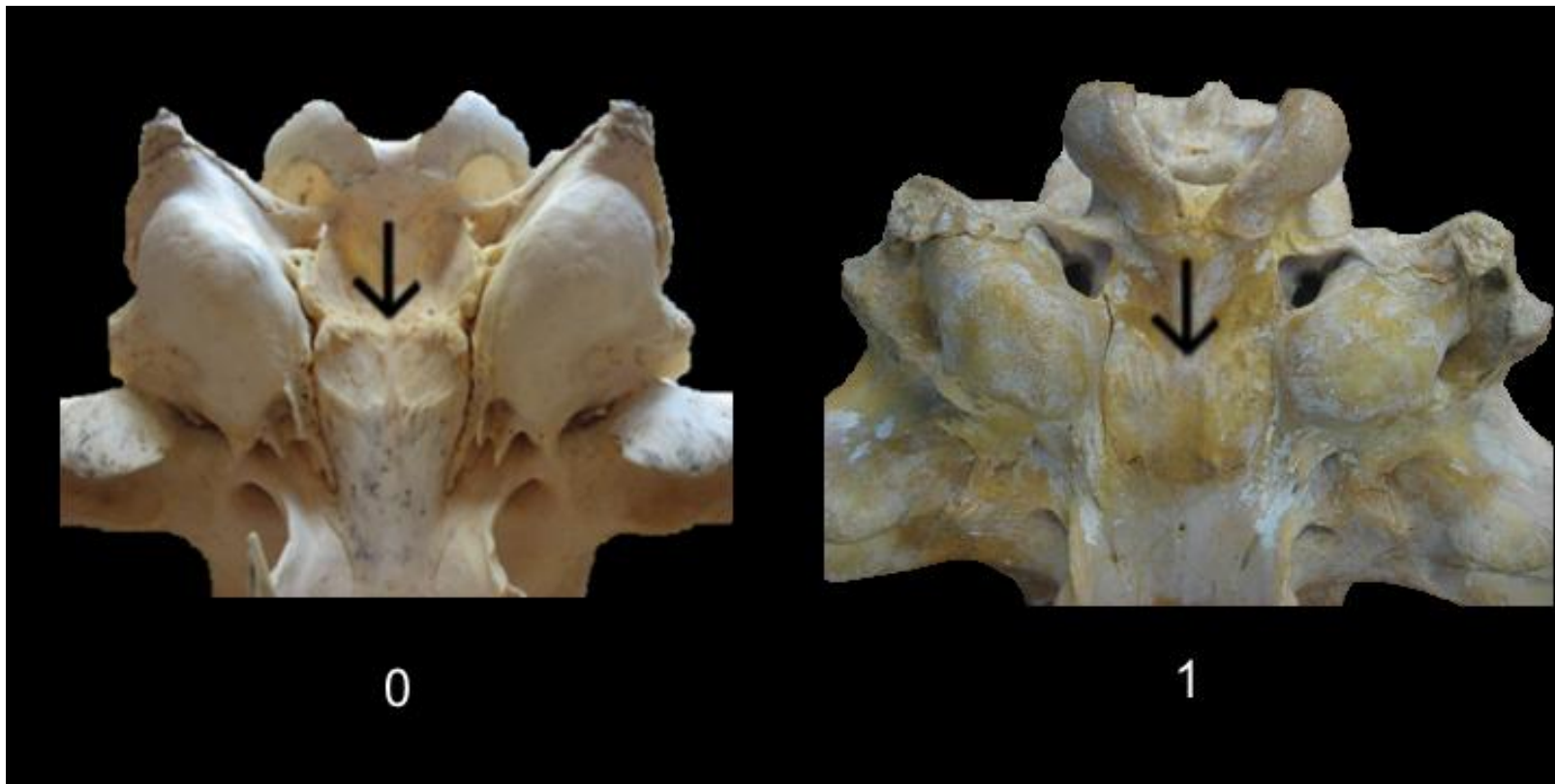


35. I3 has multiple cusps (0) or has a single cusp (1).





36. Occipital basisphenoid suture protrudes ventrally (0) or does not protrude (1).





37. m1 carnassial notch linguall shallow (1) or deep (1).



38. Paroccipital not reduced (0) or reduced or nearly absent (1).



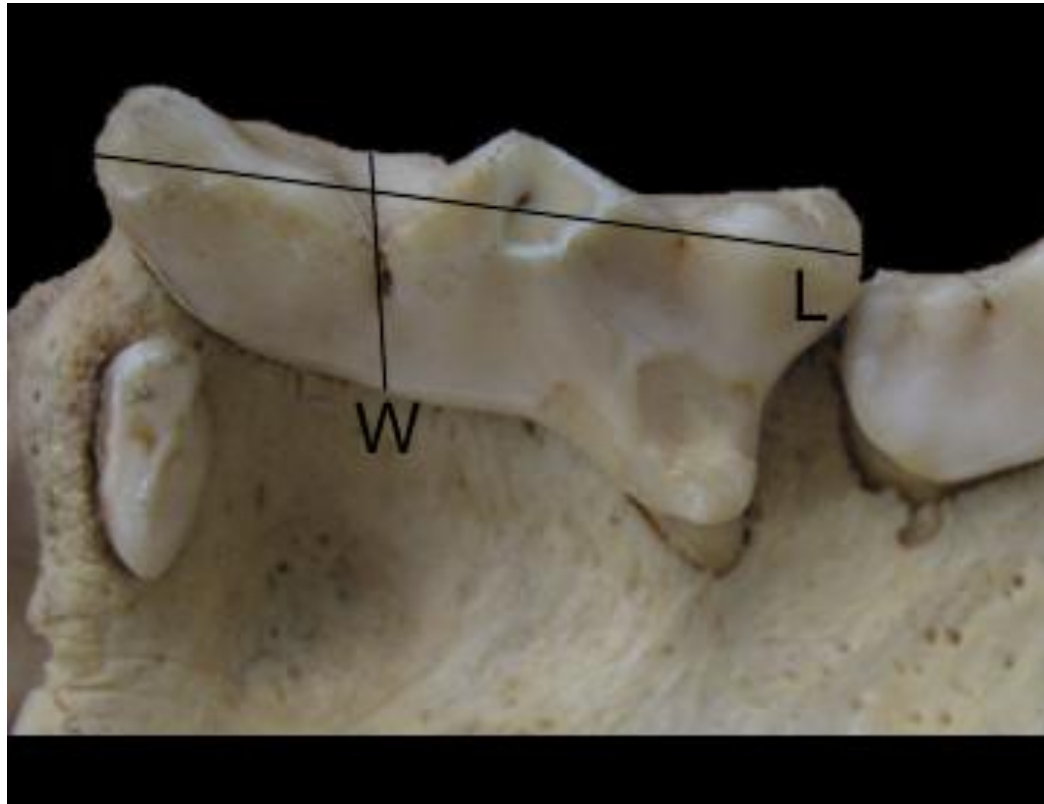
39. p4 has single posterior cusp (first posterior accessory cusp) (0) or multiple posterior cusps (first and secondary accessory cusp) (1).



40. Upper canine lacks a dorso-ventral ridge (0) or has a dorso-ventral ridge



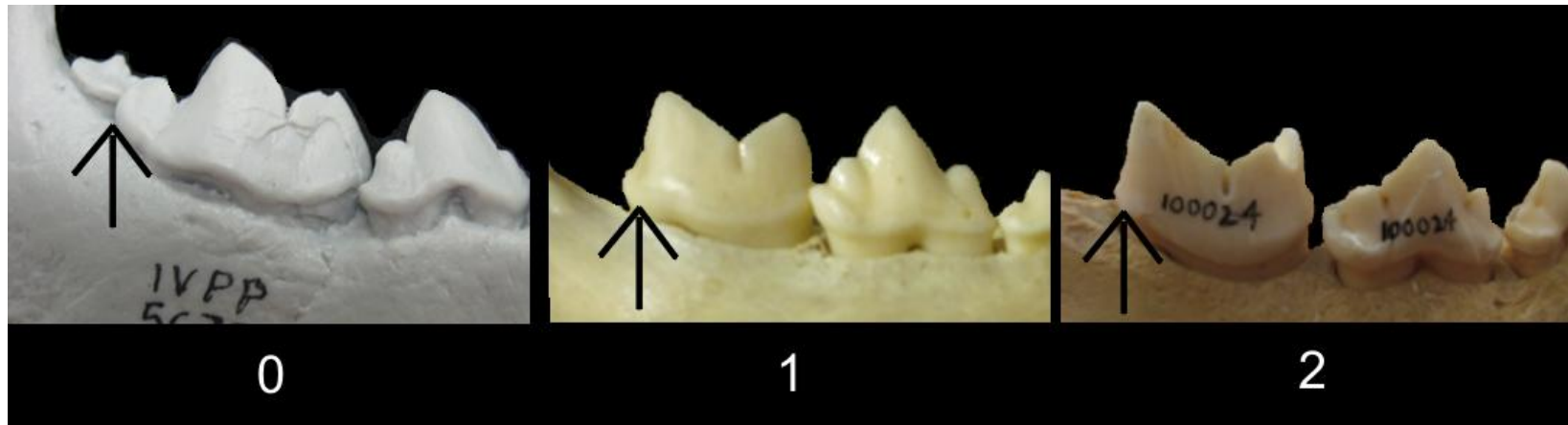
41. Ratio of length and width at the carnassial notch of the carnassials (P4) is greater than 3.2 (0), is between 1.0 and 3.4 (1), or is less than 3.2 (2). Measurements were taken using digital calipers, with the length being measured at the most anterior and posterior points of the tooth and the width across the carnassial notch.



## Appendix C- Character descriptions using *Metailurus* ssp. as the outgroup

Dental terminology from Hershkovitz (1971) and Salles (1992); Characters 22, 23, and 24 from Salles (1992); Characters 12, 13, and 14 modified from Christiansen and Harris (2009); Character 16 modified from Christiansen (2008); Character 18 and 19 from Merriam and Stock (1932)

1. p2 is present (0) or absent (1).
2. m2 is present (0) or absent (1).
3. Large metaconid on m1 (0), reduced (1), or absent (2).



4. p1 present (0) or absent (1).
5. Ratio of distance between mastoid and paroccipital process to skull length is greater than 0.04 (0), between 0.015 and 0.06 (1), or less than 0.04 (2).
6. Process between entotympanic and ectotympanic (above Vidian nerve canal) does not (0) or does protrude ventrally (1).
7. Ratio of m1 length to width is greater than 4.0 (0) or less than 4.0 (1).
8. Protocone is wider than anterior parastyle (0) or is equal or thinner in width (1).
9. Occipital is flat (0) or has depressions (1).
10. Suture between occipital and auditory bulla not visible ventrally and tucks below bulla (0) or visible ventrally (1).
11. Foramen ovale does not intersect with the pterygoid process of the basisphenoid (0) or does intersect (1).

12. Angle between the maxilla and postorbital process is greater than  $90^\circ$  (0), is between  $80^\circ$ - $115^\circ$  (1), or is less than  $90^\circ$  (2). This measurement was achieved by drawing a straight line along the maxillary tooth row from the P2 to M1 and then measuring the angle of the postorbital process to this line.
13. Frontal nasal suture is posterior to maxillary frontal suture (0), is level with the maxillary frontal suture (1), or is anterior to the maxillary frontal suture (2).
14. Ratio of the distance between the postorbital process and the posterior-most point of the maxillary frontal suture is less than 0.2 (0) or is between 0.13-0.35 (1). This measurement was achieved by drawing a straight line between the posterior-most points of the maxillary frontal sutures and then measuring the distance from the postorbital process at its lateral-most point to this line.
15. Infraorbital foramen is not visible in lateral view (0) or is visible (1).
16. Lacrimal process absent (0) or present (1).
17. Foramen rotundum not visible in lateral view (0) or visible (1).
18. Ratio of length of I2 to I3 is greater than 2.0 (0), is between 2.4-1.0 (1), or is less than 2.0 (2).
19. Ratio of distance between postorbital process and frontal parietal suture to skull length is less than 0.25 (0), is between 0.17-0.35 (1), or greater than 0.25. This measurement was made by extending a line perpendicular to the frontal parietal suture from the postorbital process and measuring the distance.
20. Posterior palatine foramen is anterior to the carnassial notch but posterior to the carnassial (0), or is posterior to the carnassial notch (1).
21. Ratio of diameter of hypoglossal foramen to skull length is greater than 0.023 (0), is between 0.009-0.027 (1), or less than 0.02 (2).
22. Parastyle on P3 present (0), well developed (1), or absent (2).
23. P3 has multiple posterior cusps (metacone and accessory cusp) (0) or a single cusp (metacone) (1).
24. Ratio of upper canine length to skull length is less than 0.2 (0), or is between 0.07-0.27 (1), or is greater than 0.2 (2).
25. p3 paraconid absent (0) or present (1).
26. p4 paraconid smaller than metaconid (0) or similar in size (1).
27. Paroccipital process extends ventrally beyond bullae height (0) or does not extend above bullae height (1).
28. Angle between paroccipital process and occipital condyle is greater than  $95^\circ$  (0) or is between  $87^\circ$ - $112^\circ$  (1). This measurement was taken by measuring the intersection between a line drawn bisecting the paroccipital process and the dorsal-most trajectory of the occipital condyle.

- 29. Auditory bullae intersect with the posterior-most point of the post glenoid process (0) or do not intersect (1).
- 30. Lateral side of mastoid process does not intersect with lambdoidal crest (0) or does intersect (1).
- 31. Foramina on lateral palatine spaced at medium distance (0), spaced very far apart (1), or nearly overlap or have completely merged (2).
- 32. Occipital basisphenoid suture does not protrude ventrally (0) or does protrude (1).
- 33. p4 has single posterior cusp (first posterior accessory cusp) (0) or multiple posterior cusps (first and secondary accessory cusp) (1).
- 34. Upper canine lacks a dorso-ventral ridge (0) or has a dorso-ventral ridge (1).



Appendix D- Character descriptions using *Proailurus lemanensis* as the outgroup

Dental terminology from Hershkovitz (1971) and Salles (1992); Characters 20 and 21 from Salles (1992); Character 13 modified from Christiansen and Harris (2009); Character 15 modified from Christiansen (2008); Character 18 modified Merriam and Stock (1932)

1. Presence of P1 (0) or absence (1).
2. m1 metaconid present (0) or absent (1).
3. Presence of m2 (0) or absence (1).
4. Presence of p2 (0) or absence (1).
5. Presence of p1 (0) or absence (1).
6. Ratio of distance between mastoid and paroccipital process to skull length is greater than 0.04 (0), is between 0.018-0.06 (1), or less than 0.04 (2).
7. Angle of auditory bulla is less than 32° (0), is between 22°-48° (1), or is greater than 32° (2). This angle was measured by creating a straight line between the center of the occipital condyles and premaxilla and another straight line from the center of the paroccipital process to the anterior-most point on the bulla. The angle measured was between the intersection of these two lines.
8. Ratio of m1 length to width is greater than 2.0 (0) or between 1.0-2.3 (1).
9. Protocone is wider than anterior parastyle (0) or is equal or thinner in width (1).
10. Occipital is flat (0) or has depressions (1).
11. Superior orbital fissure is not visible in ventral view (0) or is visible (1).
12. Foramen ovale does not intersect with the pterygoid process of the basisphenoid (0) or does intersect (1).
13. Angle between the maxilla and postorbital process is greater than 90° (0), is between 73°-115° (1), or is less than 90° (2). This measurement was achieved by drawing a straight line along the maxillary tooth row from the P2 to M1 and then measuring the angle of the postorbital process to this line.
14. Infraorbital foramen not visible in lateral view (0) or visible (1).
15. Lacrimal process absent (0) or present (1).
16. Mastoid process is reduced (0) or well developed (1).
17. Auditory bullae do not intersect with the posterior-most point of the post glenoid process (0) or do intersect (1).

18. Posterior palatine foramen is anterior to the carnassial (0), is anterior to the carnassial notch but posterior to the carnassial (1), or is posterior to the carnassial notch (1).
19. Ratio of diameter of hypoglossal foramen to skull length is less than 0.02 (0), or is between 0.01-0.027 (1).
20. Parastyle on P3 is absent (0), reduced (1), or well developed (2).
21. Metacone reduced in P3 (0), developed (1), or has additional posterior accessory cusp (2).
22. Paraconid of p3 is absent (0) or present (1).
23. First and second posterior accessory cusps present on p3 (0) or just first posterior accessory cusp present (1).
24. Paroccipital process extends ventrally beyond bullae height (0) or does not extend above bullae height (1).

25. Angle between paroccipital process and occipital condyle is less than  $95^\circ$  (0), is between  $87^\circ$ - $112^\circ$  (1), or is greater than  $95^\circ$  (2). This measurement was taken by measuring the intersection between a line drawn bisecting the paroccipital process and the dorsal-most trajectory of the occipital condyle.



26. Lateral side of mastoid process does not intersect with lambdoidal crest (0) or does intersect (1).  
27. Foramen rotundum has two openings (0) or a single opening (1).  
28. Upper canine lacks a dorso-ventral ridge (0) or has a dorso-ventral ridge (1).

## Appendix E-Character descriptions using *Pseudaelurus validus* as the outgroup

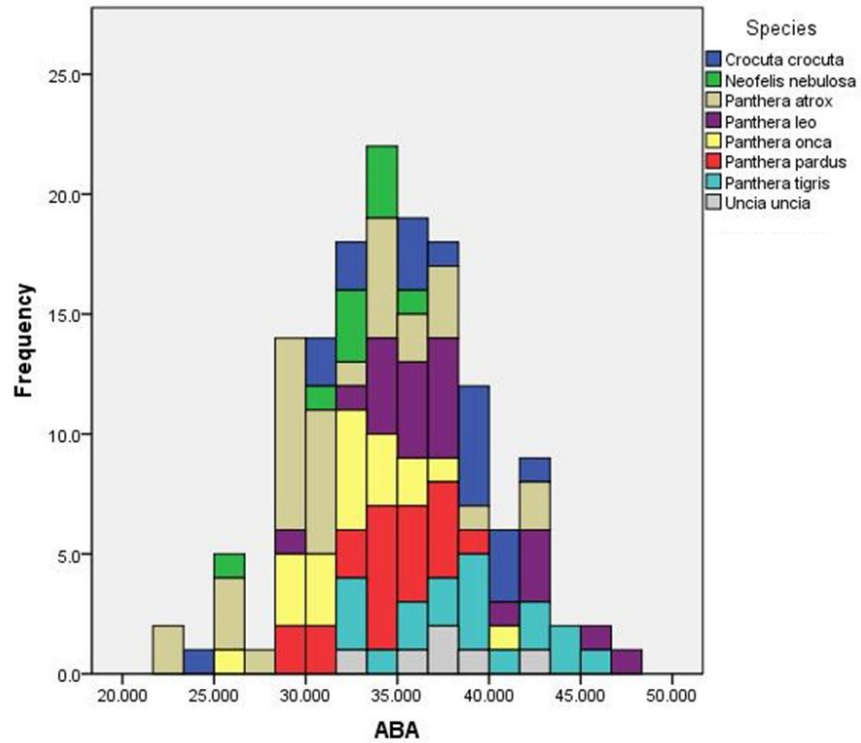
Dental terminology from Hershkovitz (1971) and Salles (1992); Character 18 modified from Salles (1992); Characters 9 and 10 modified from Christiansen and Harris (2009); Character 11 modified from Christiansen (2008); Characters 15 and 16 modified from Merriam and Stock (1932)

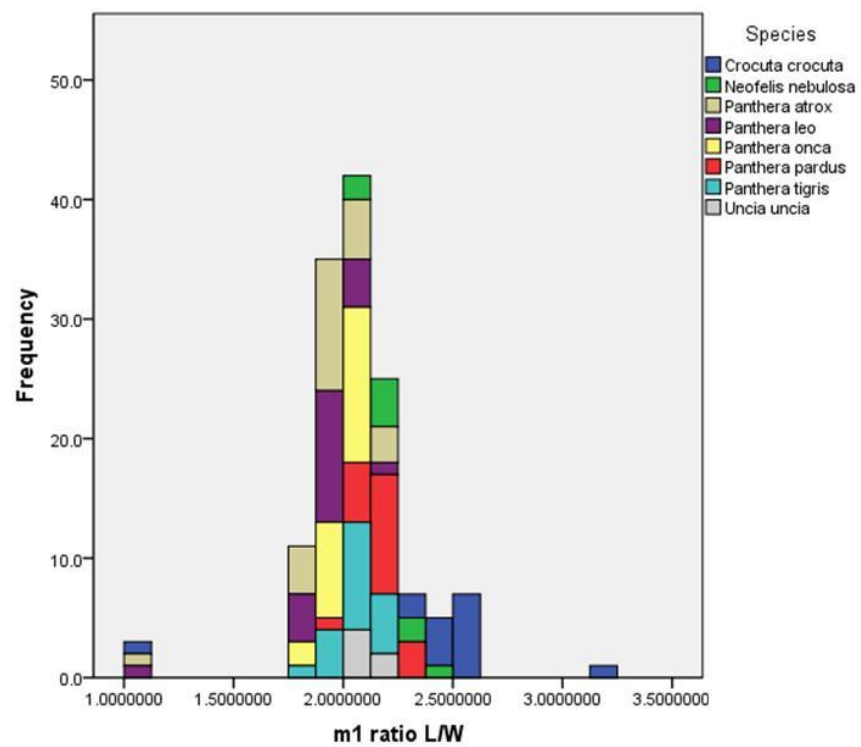
1. Ratio of distance between mastoid and paroccipital process to skull length is greater than 0.04 (0), is between 0.018-0.082 (1), or less than 0.04 (2).
2. Angle of auditory bulla is less than 27° (0), is between 22°-43° (1), or is greater than 27° (2). This angle was measured by creating a straight line between the center of the occipital condyles and premaxilla and another straight line from the center of the paroccipital process to the anterior-most point on the bulla. The angle measured was between the intersection of these two lines.
3. Process between entotympanic and ectotympanic (above vidian nerve canal) does not (0) or does protrude ventrally (1).
4. Ratio of m1 length to width is greater than 2.0 (0) or is between 1.0-2.4 (1).
5. P4 protocone is wider than anterior parastyle (0) or is equal or thinner in width (1).
6. Suture between occipital and auditory bulla not visible ventrally and tucks below bulla (0) or visible ventrally (1).
7. Tympanohyal pit and stylomastoid foramen share a single opening (0) or are separate (1).
8. Foramen ovale does not intersect with the pterygoid process of the basisphenoid (0) or does intersect (1).
9. Angle between the maxilla and postorbital process is between 80°-115° (0) or is less than 90° (1). This measurement was achieved by drawing a straight line along the maxillary tooth row from the P2 to M1 and then measuring the angle of the postorbital process to this line.
10. Frontal nasal suture is posterior to maxillary frontal suture (0), is level with the maxillary frontal suture (1), or is anterior to the maxillary frontal suture (2).
11. Lacrimal process absent (0) or present (1).
12. Foramen rotundum visible in lateral view (0) or not visible (1).
13. Mastoid process reduced (0) or well developed (1).
14. Angle between the hypoglossal and jugular foramina is less than 40° (0) or is between 18°-55° (1). This angle was measured by bisecting each foramen and measuring the angle at which both lines intersected.

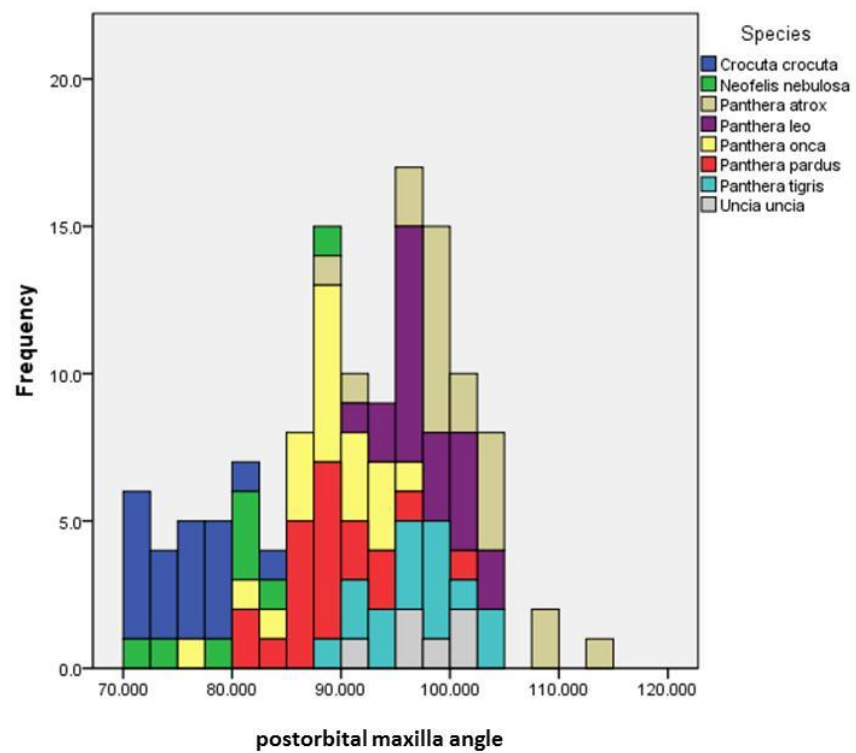
15. Ratio of distance between postorbital process and frontal parietal suture to skull length is greater than 0.24 (0), is between 0.17-0.35 (1), or is less than 0.24 (2). This measurement was calculated by extending a line perpendicular to the frontal parietal suture from the postorbital process and measuring the distance.
16. Posterior palatine foramen is anterior to carnassial notch (0) or posterior to notch (1).
17. Ratio of diameter of hypoglossal foramen to skull length greater than 0.018 (0), is between 0.008-0.027(1), or is less than 0.018 (2).
18. First and second posterior accessory cusps are present on P3 (0) or only first accessory cusp is present (1).
19. m1 metaconid present (0) or absent (1).
20. Paroccipital process extends ventrally beyond bullae height (0) or does not extend above bullae height (1).
21. Auditory bullae do not intersect with the posterior-most point of the post glenoid process (0) or do intersect (1).
22. Lateral side of mastoid process does intersect with lambdoidal crest (0) or does not intersect (1).
23. Occipital basisphenoid suture have ridges that run vertically (0), horizontally (1), or lack ridging (2).
24. Paroccipital process curves anteriorly over the auditory bulla (0) or does not curve anteriorly (1).
25. p4 has multiple posterior cusps (one may be smaller than the other) (0) or has a single cusp (1).
26. Postorbital process is highly reduced (0) or well developed (1).
27. Foramen ovale shares an opening with the foramen rotundum (0) or two separate openings present (1).
28. Foramen rotundum has two openings (acts as “tunnel”) or has a single opening (1).
29. Upper canine lacks a dorso-ventral ridge (0) or has a dorso-ventral ridge (1).
30. Ratio of the distance between the postorbital process and the posterior-most point of the maxillary frontal suture is less than 0.15 (0), is between 0.08-0.23 (1), or is greater than 0.15 (2). This measurement was achieved by drawing a straight line between the posterior-most points of the maxillary frontal sutures and then measuring the distance from the postorbital process at its lateral-most point to this line.

Appendix F- Histograms of linear measurements deemed statistically significant by stepwise discriminant analysis

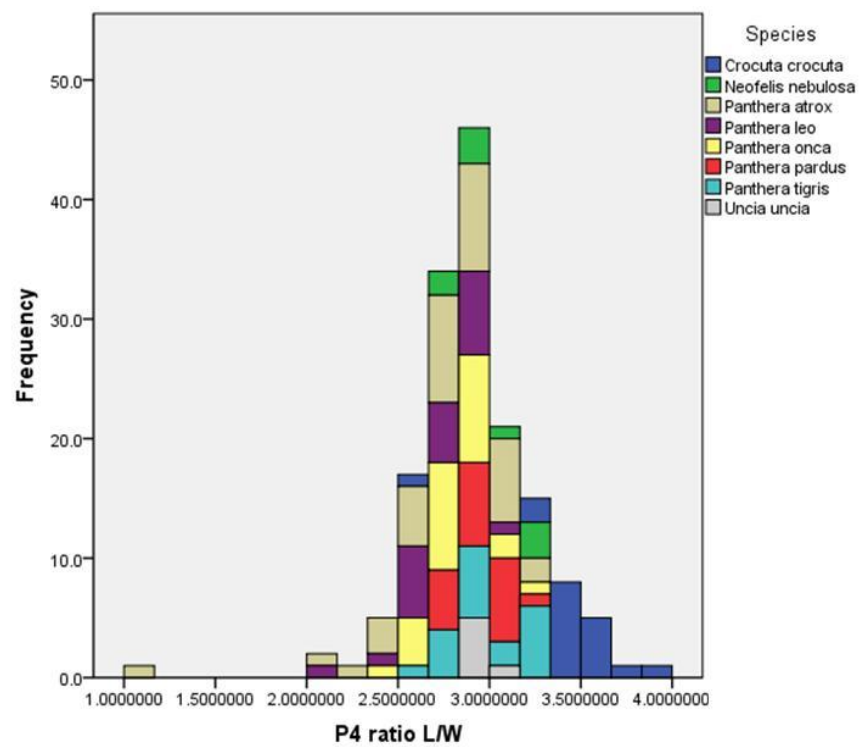
*Crocota crocuta*

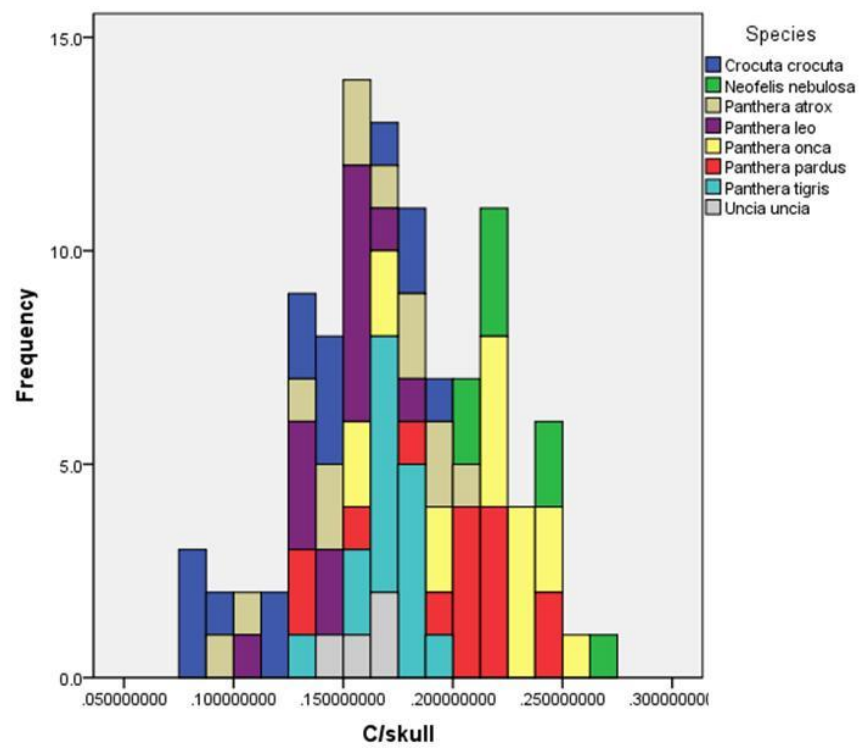


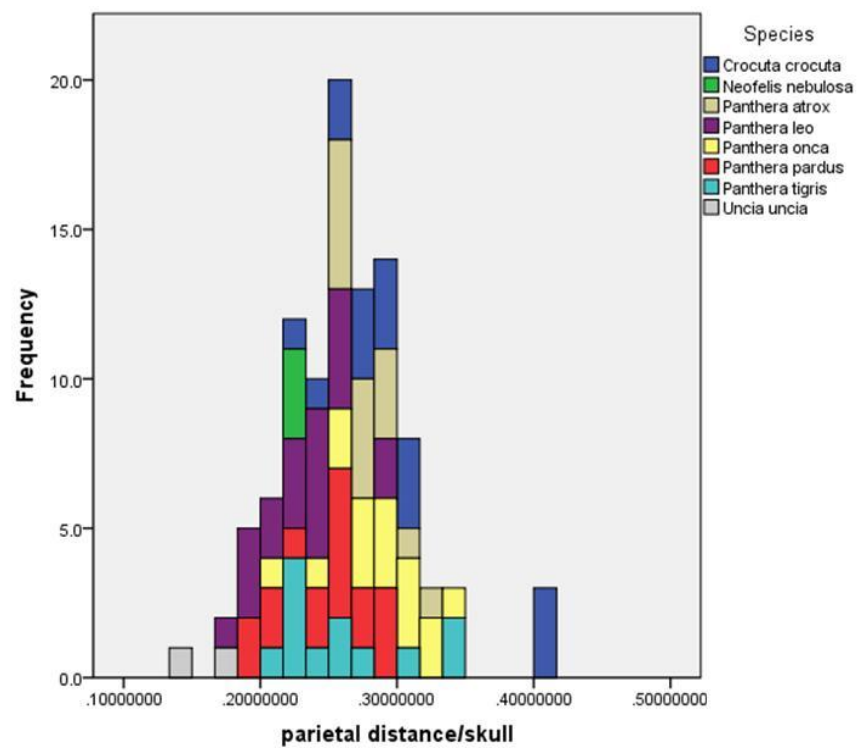


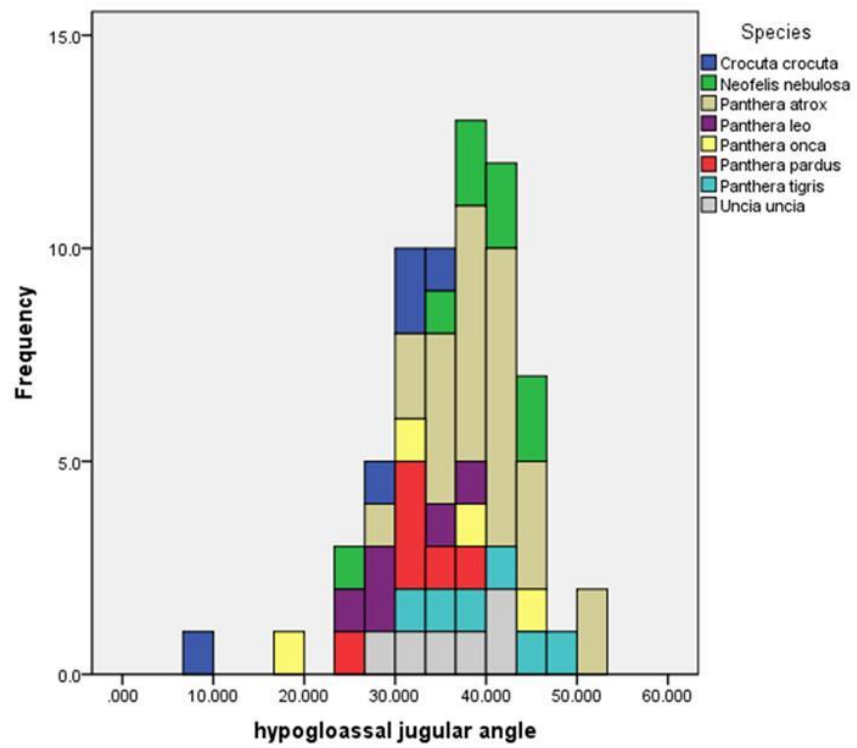




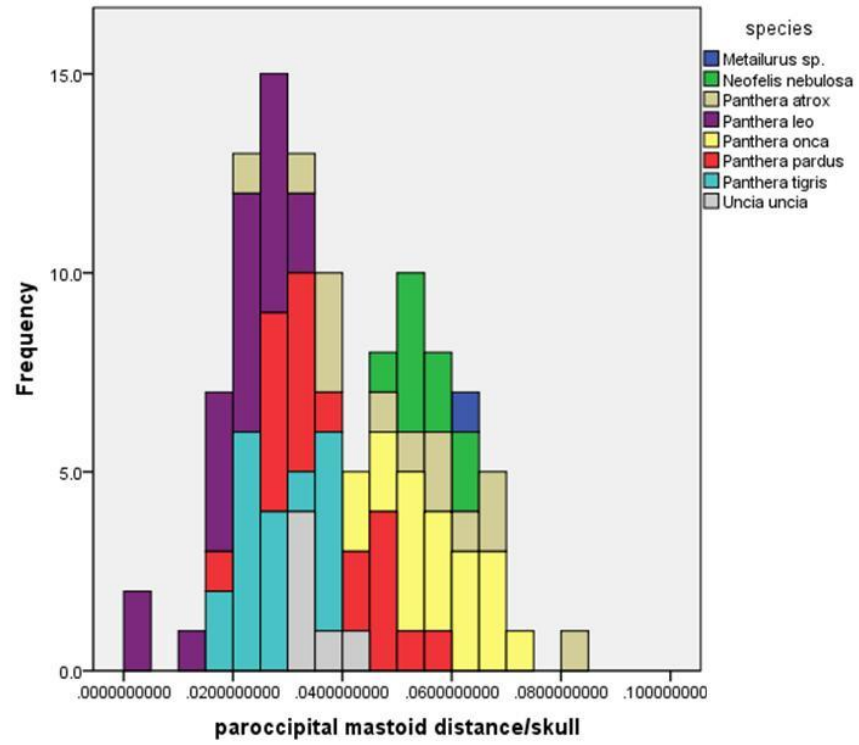


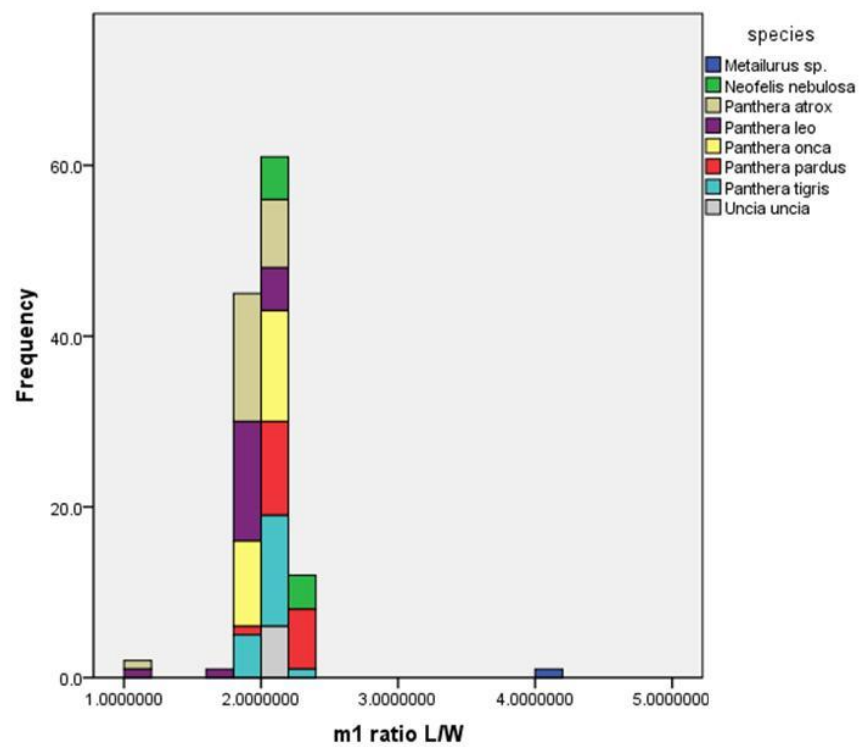


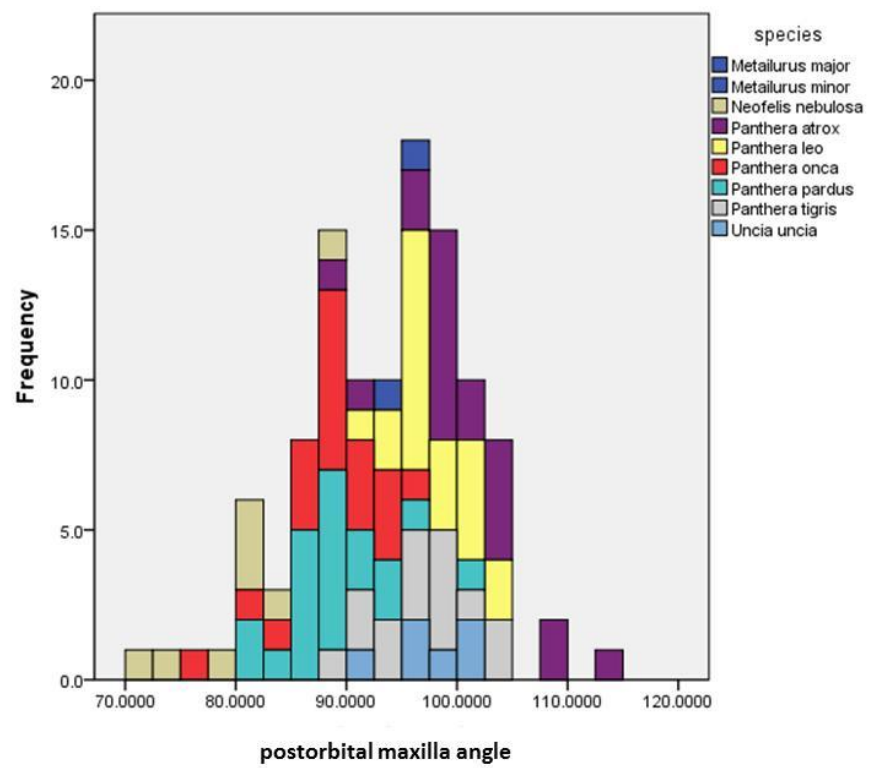


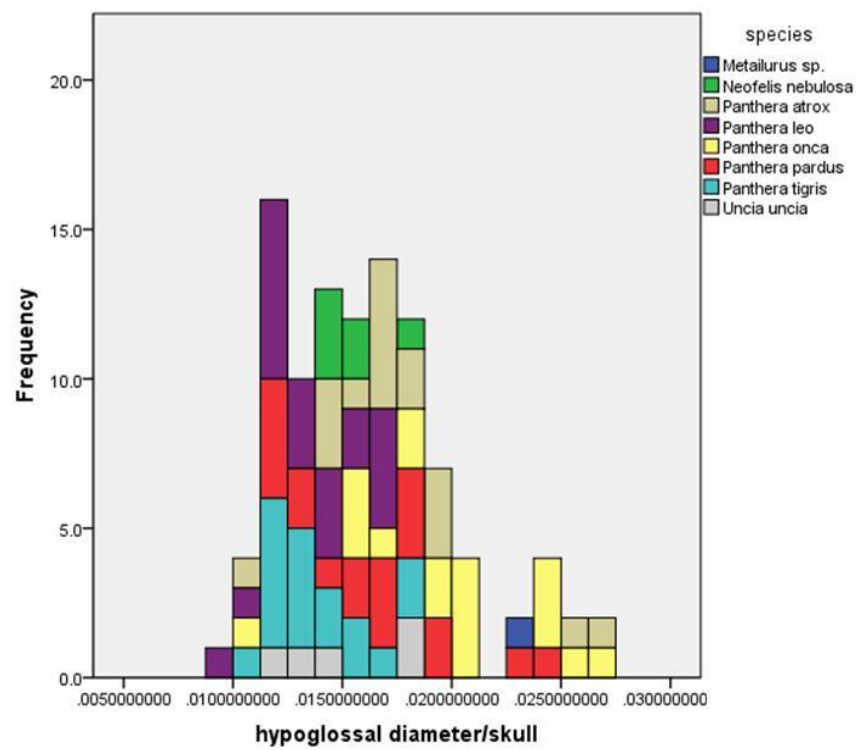


*Metailurus* ssp.

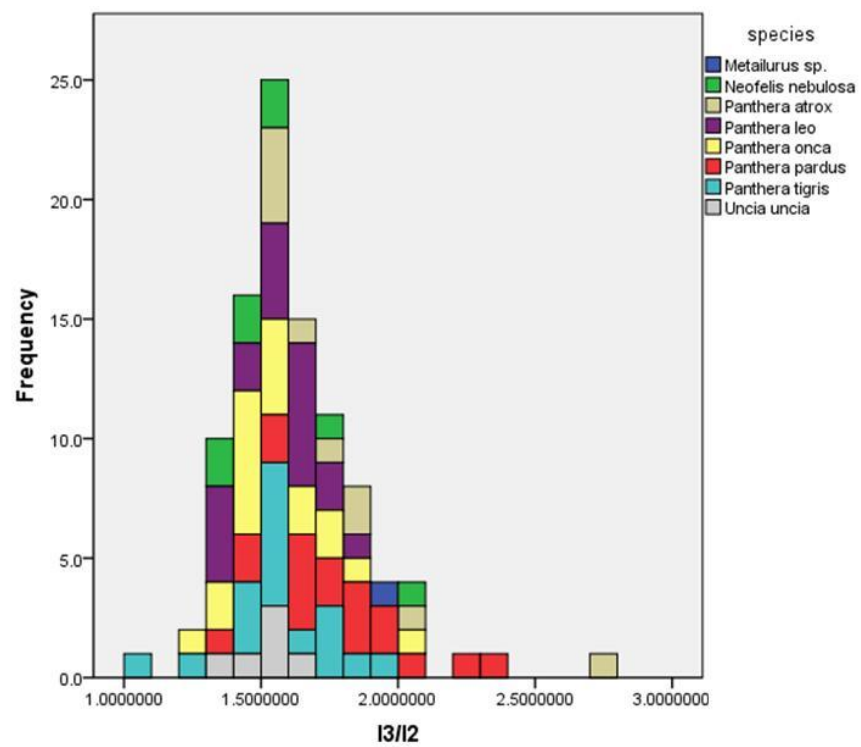


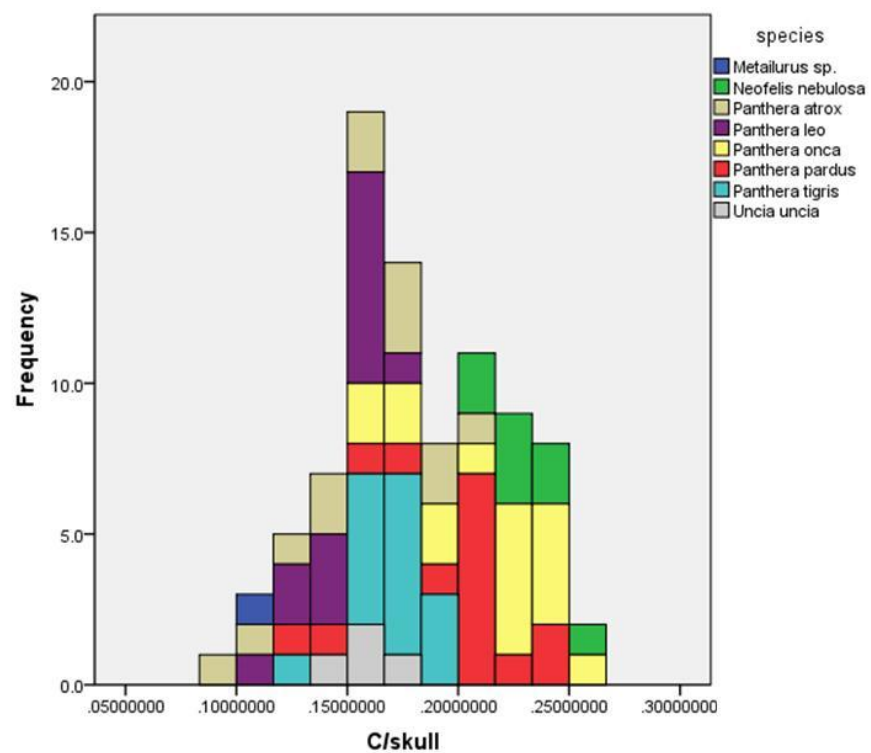


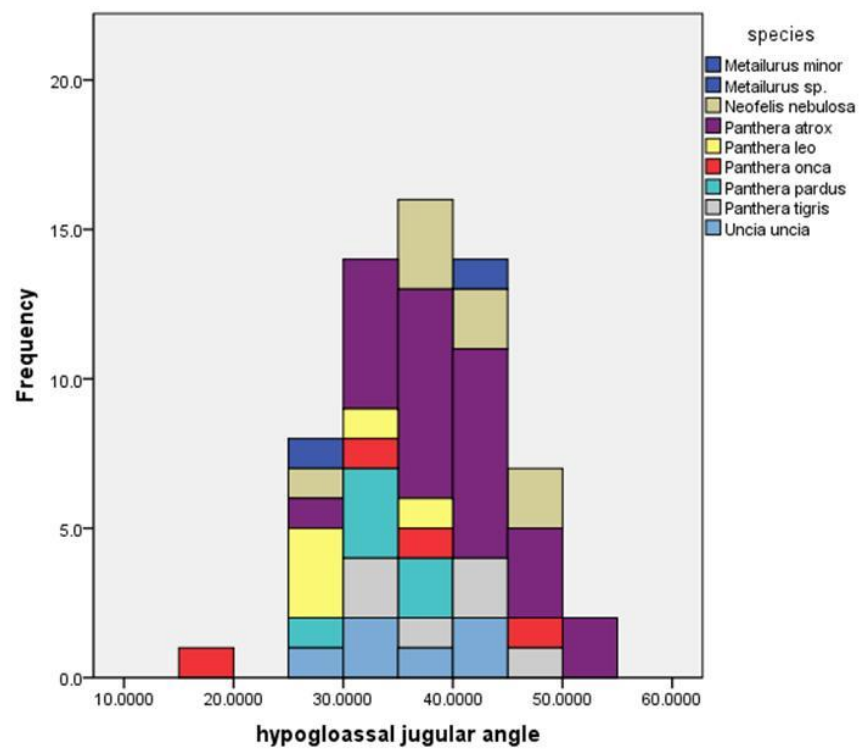


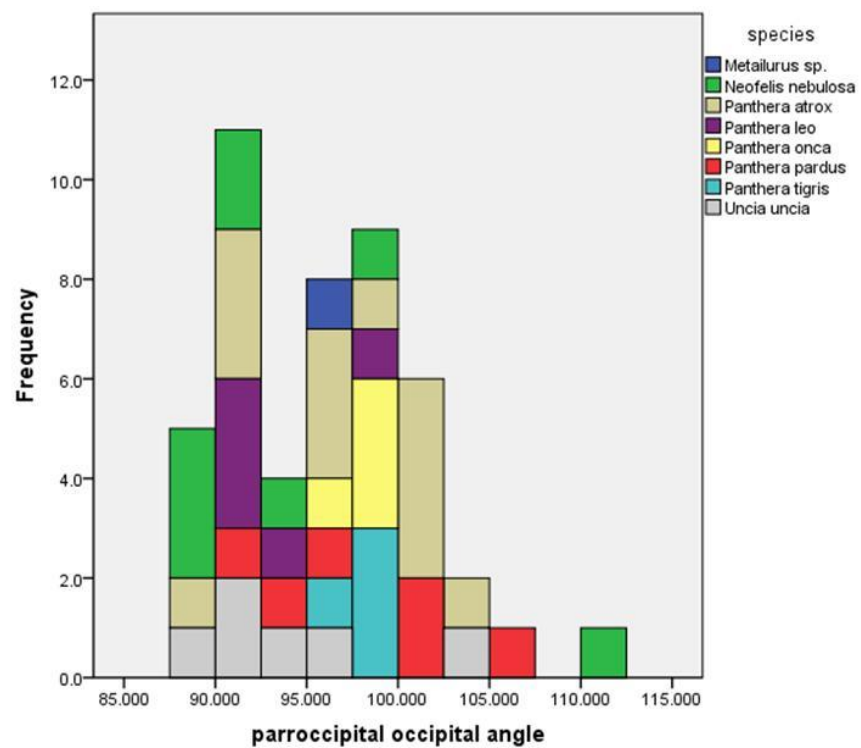


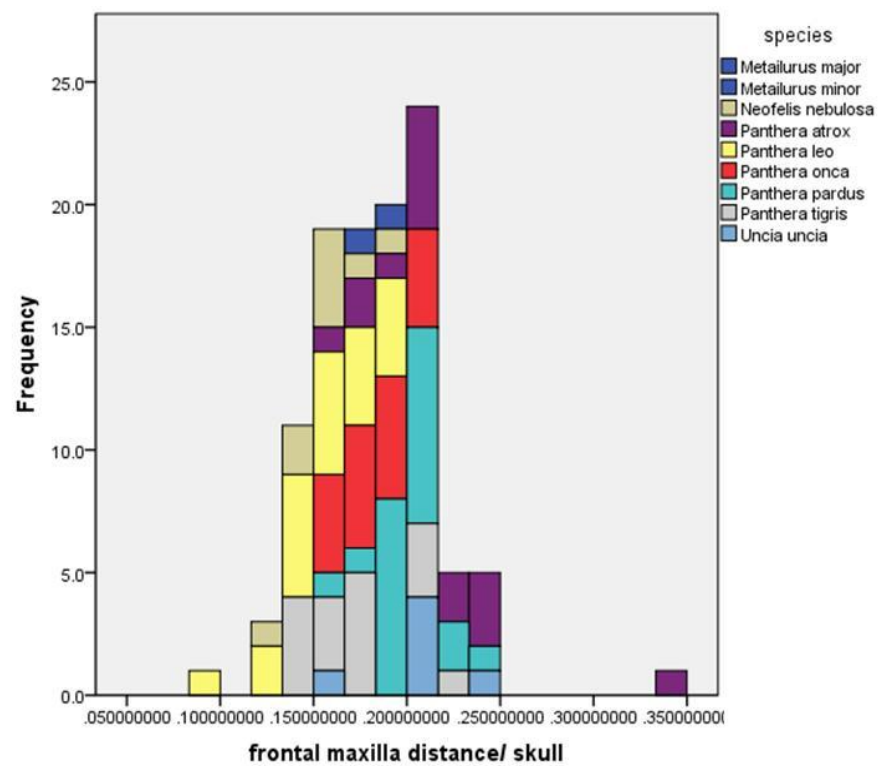


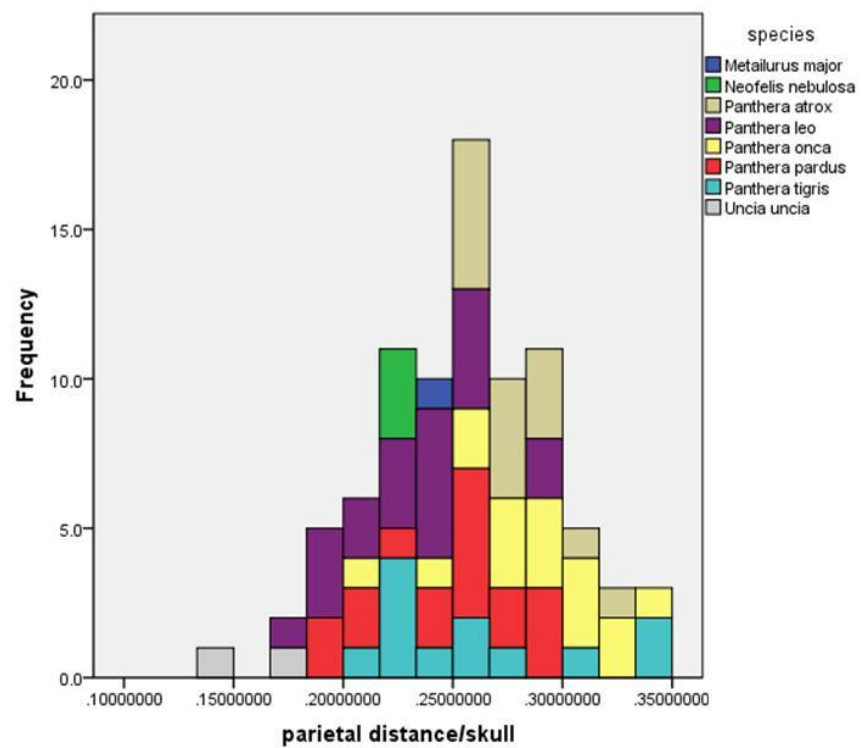




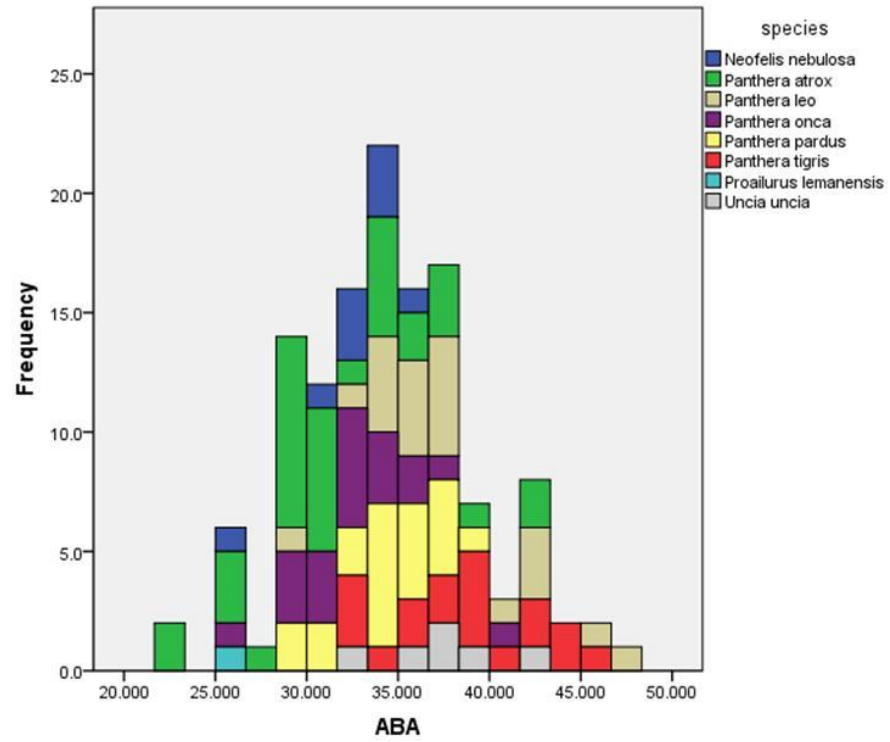


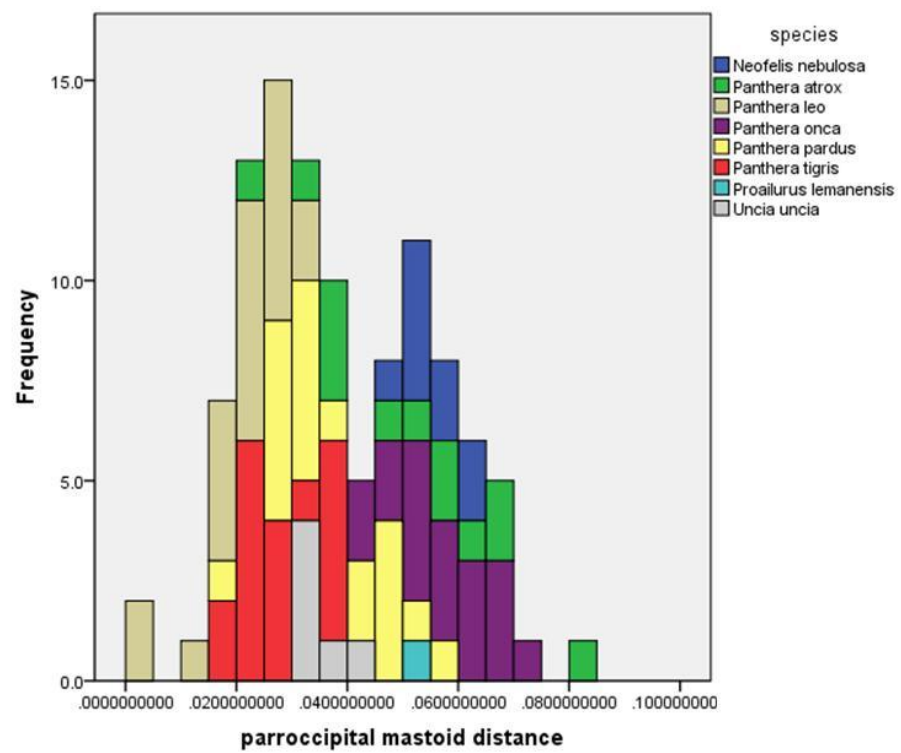




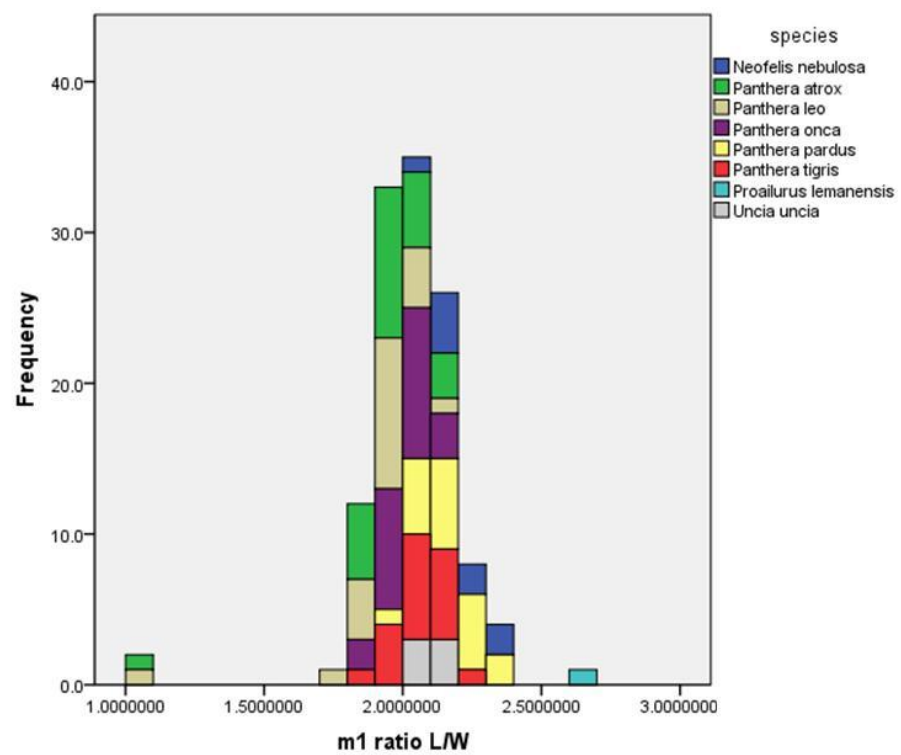


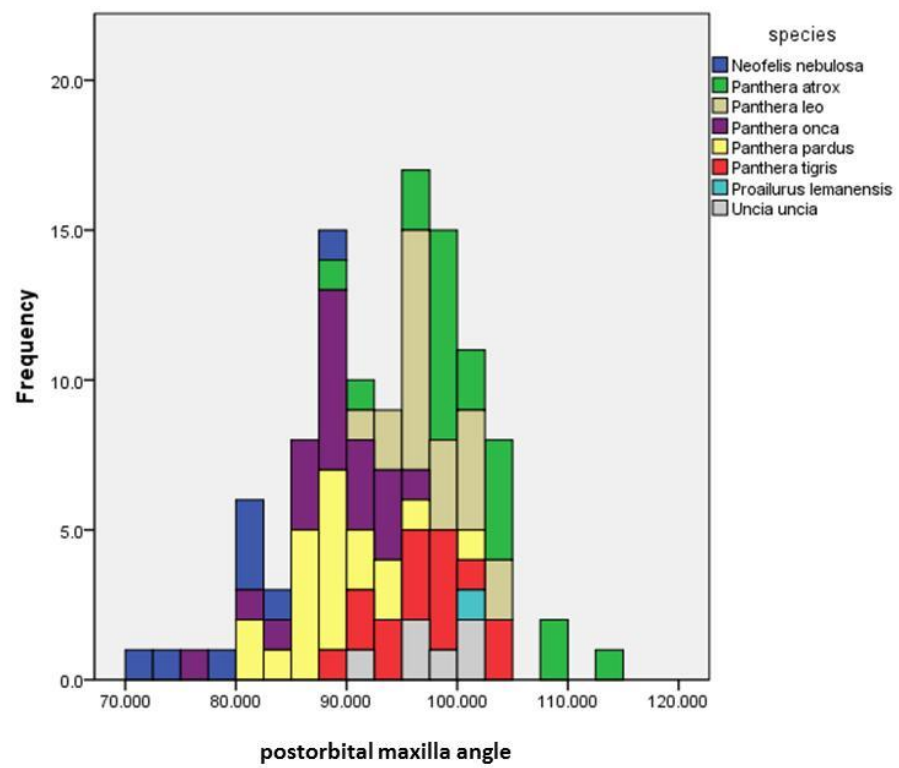
*Proailurus lemanensis*

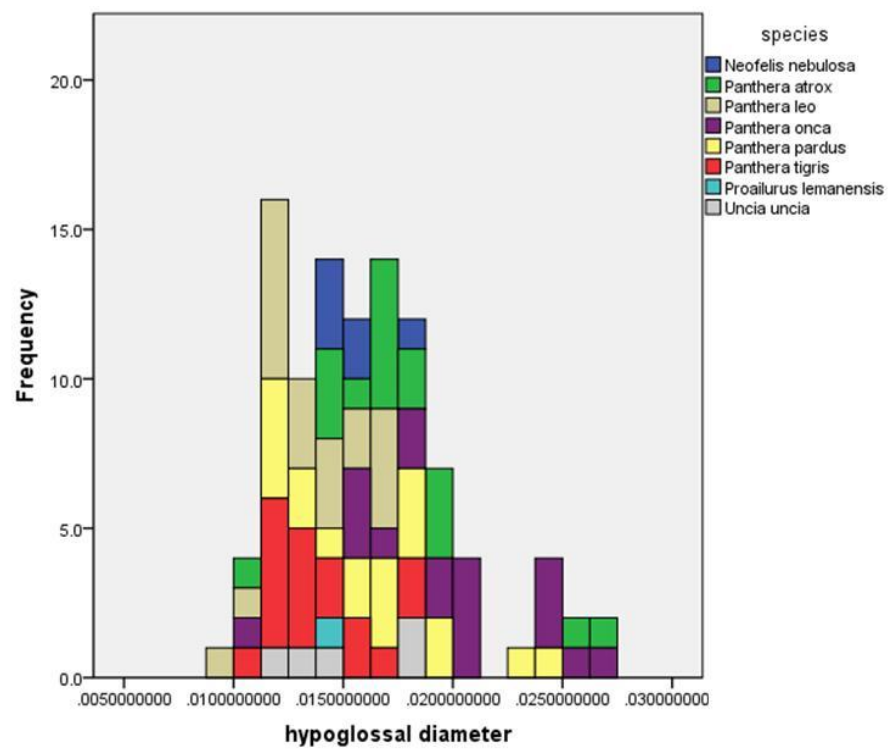


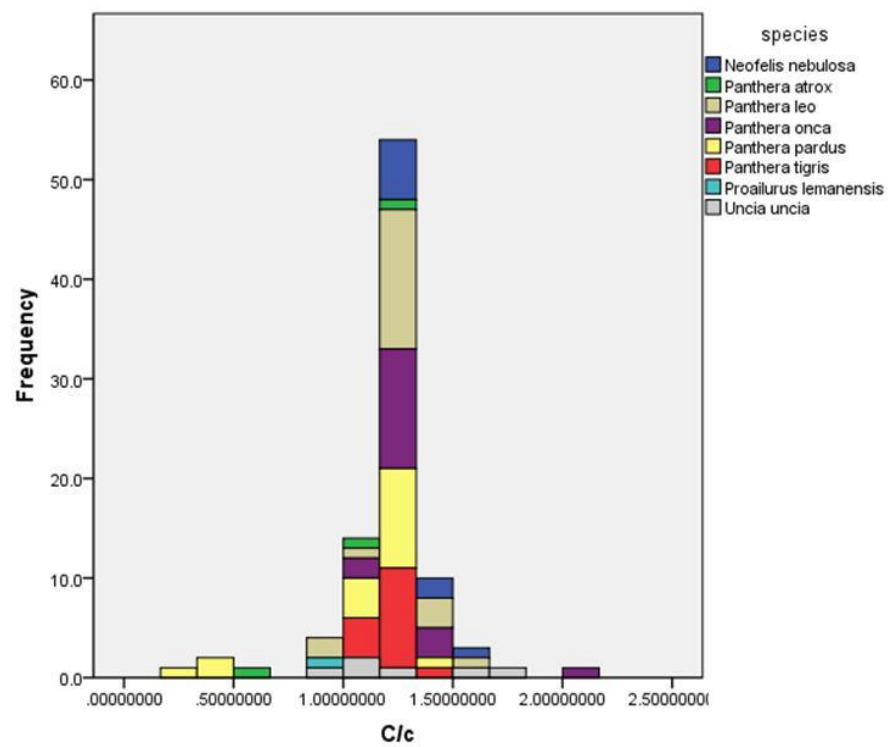


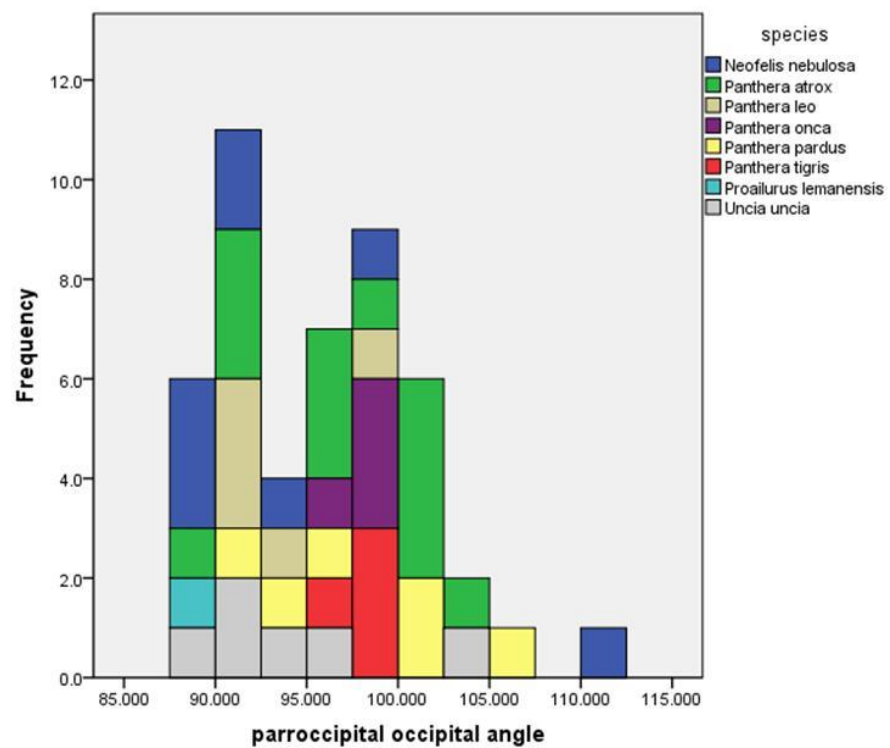




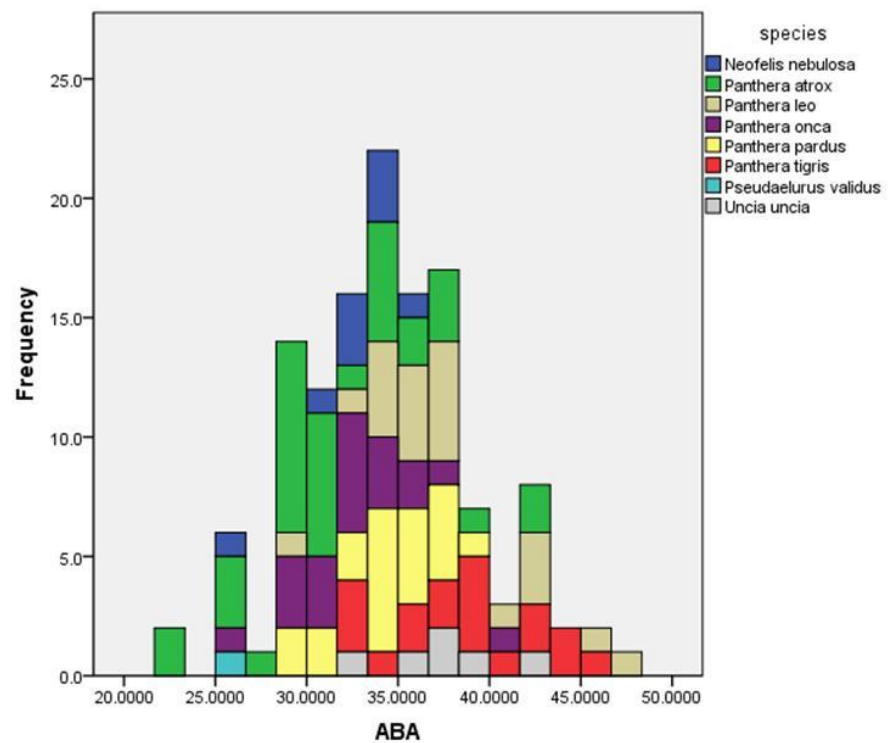


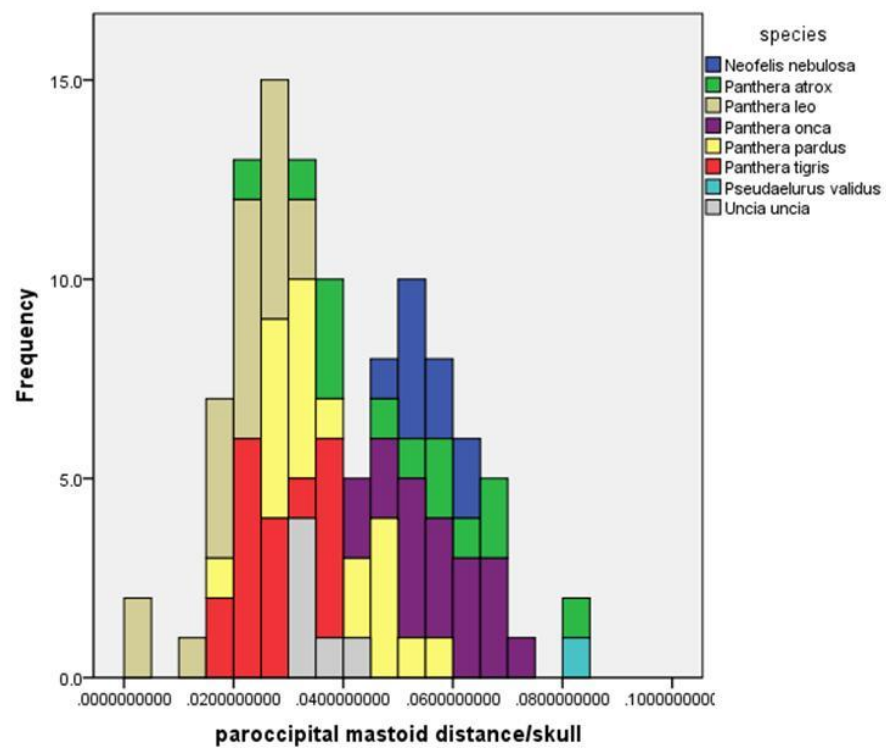


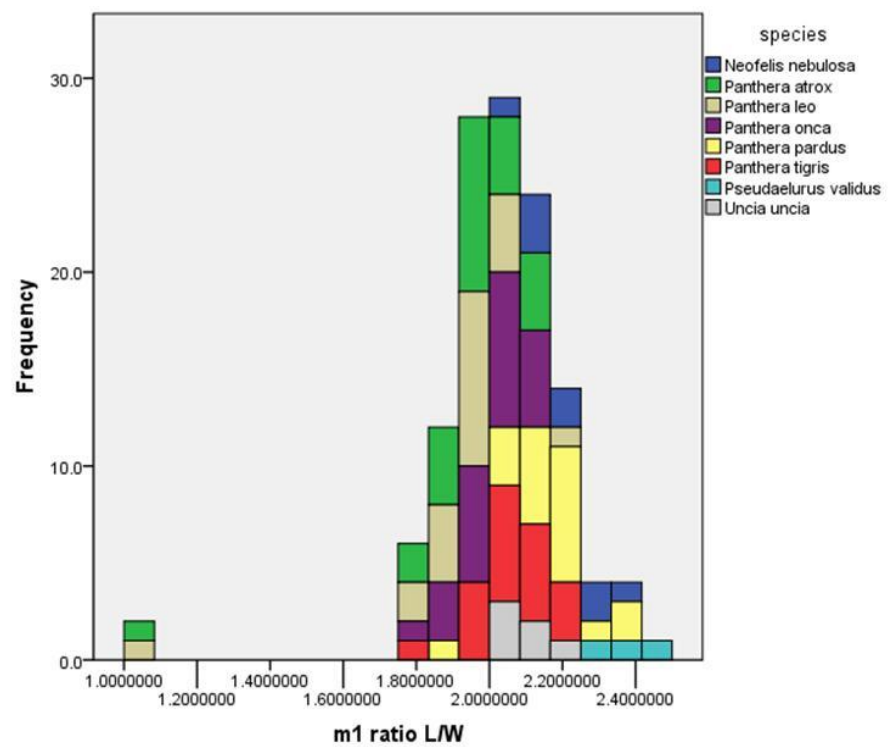




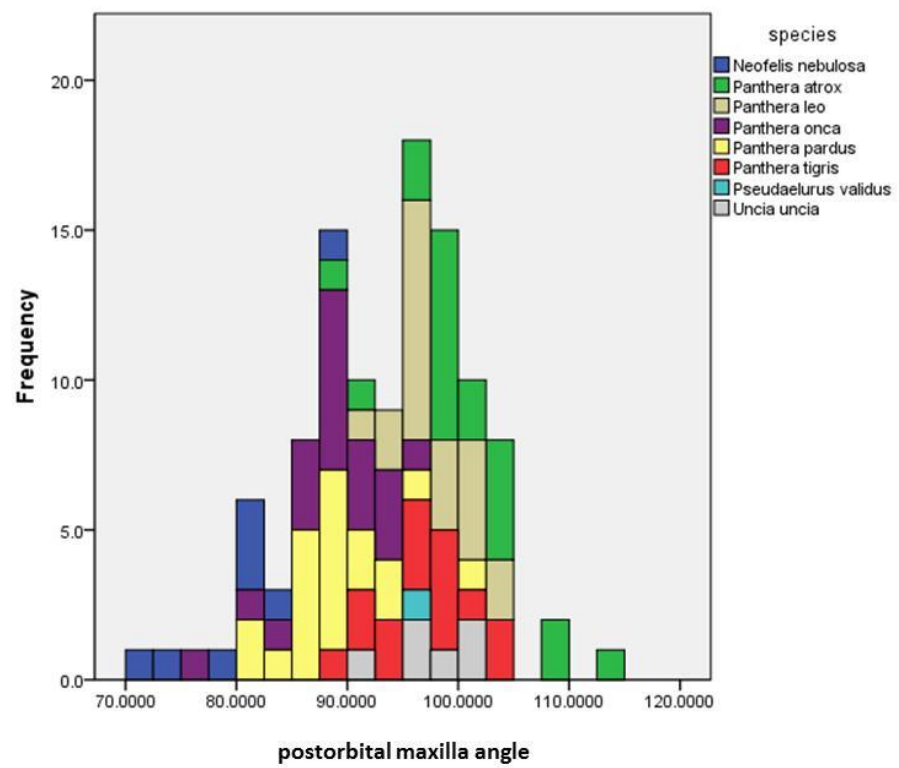
*Pseudaelurus validus*

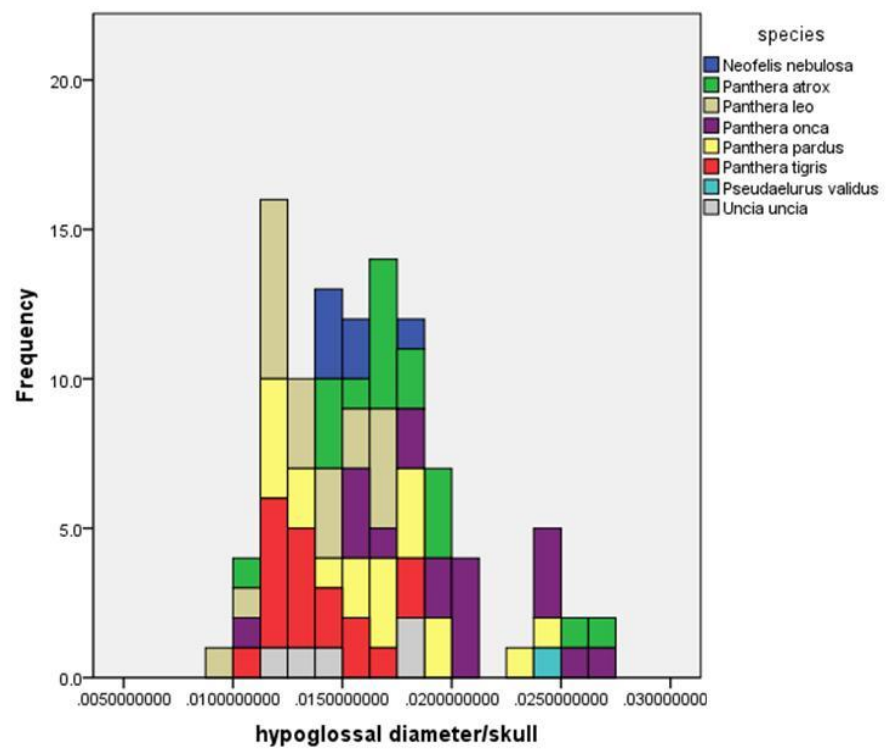


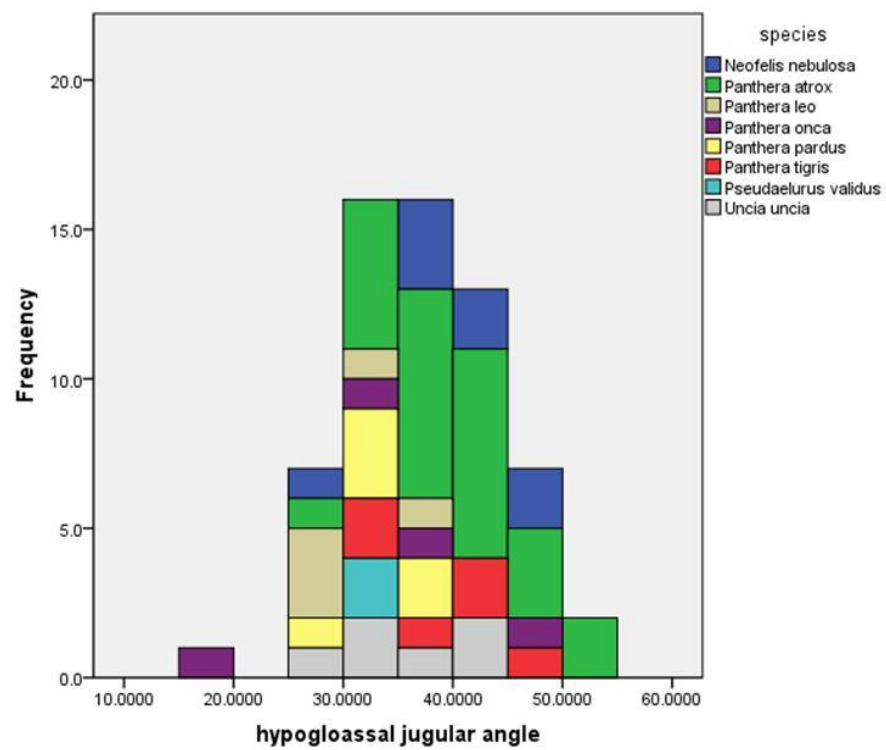


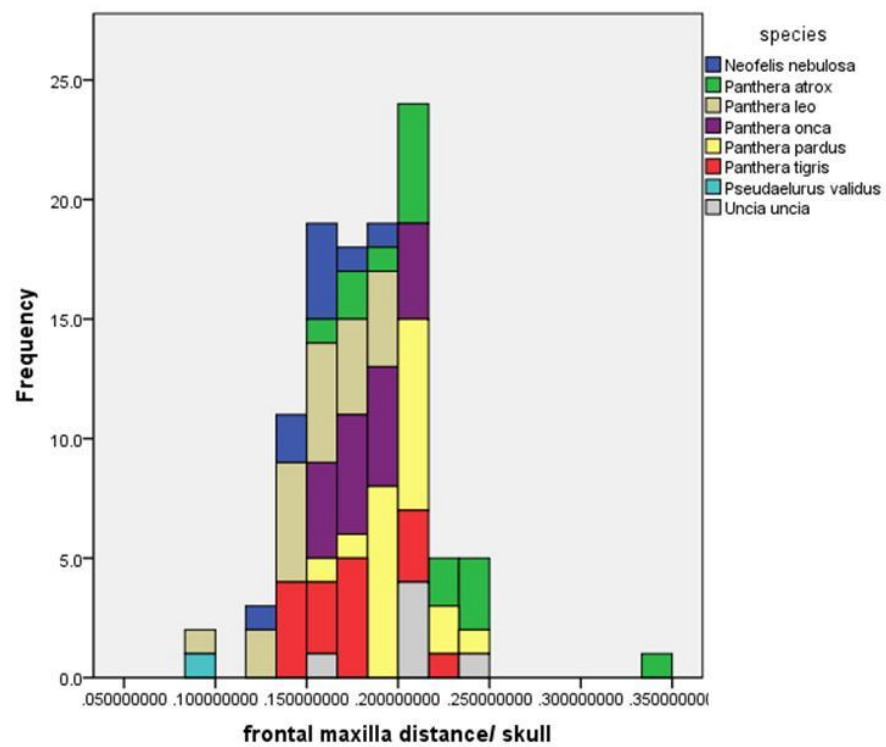


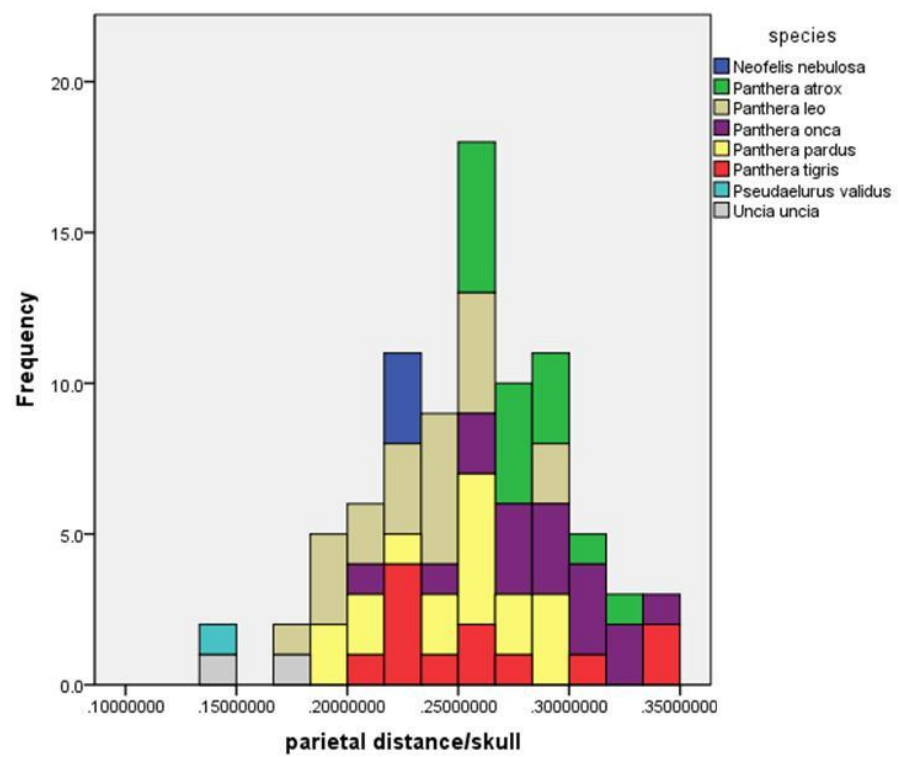














Appendix G- Character score matrices used within phylogenetic analysis for *Crocota crocuta*, *Metailurus* ssp., *Proailurus lemanensis*, *Pseudaelurus validus*, *Panthera leo*, *P. tigris*, *P. onca*, *P. pardus*, *P. atrox*, *Neofelis nebulosa*, and *Uncia uncia*.

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4																																			
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1					
<i>C. crocuta</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>P. leo</i>	0	1	1	1	2	0	0	1	1	0	0	2	0	1	1	1	1	0	1	0	1	2	1	1	2	1	0	1	1	1	0	0	2			
<i>P. tigris</i>	1	0	1	1	2	0	0	1	1	0	1	1	2	0	1	1	1	1	1	0	2	1	1	2	2	0	1	1	1	1	0	2	1			
<i>P. onca</i>	0	1	1	1	2	0	0	0	1	0	0	1	2	1	1	1	1	1	1	0	2	1	1	2	2	1	1	1	1	1	1	0	1			
<i>P. pardus</i>	0	1	1	1	1	0	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	0	1			
<i>N. nebulosa</i>	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	2	2	1	1	1	1	1			
<i>U. uncia</i>	1	0	1	1	2	0	0	1	1	1	1	2	1	1	1	1	1	1	1	1	2	1	0	1	0	1	0	1	1	1	0	0	1			
<i>P. atrox</i>	0	0	2	1	1	x	1	1	1	0	0	1	0	0	1	1	1	1	1	1	0	2	1	1	2	2	1	1	1	1	0	1	2			

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3																																			
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4		
<i>Metailurus</i> ssp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>P. leo</i>	1	1	1	1	2	1	1	0	0	1	1	0	2	0	0	1	1	2	1	1	2	1	0	0	1	1	0	1	1	1	2	0	0	0	0	
<i>P. tigris</i>	1	1	2	1	2	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	2	0	0	1	1	1	1	0	1	0	2	0	0	0		
<i>P. onca</i>	1	1	2	1	0	1	1	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0		
<i>P. pardus</i>	1	1	2	1	1	1	1	1	0	1	0	1	1	1	0	1	0	1	1	0	1	2	1	1	1	1	1	1	1	1	0	0	0	0		
<i>N. nebulosa</i>	1	1	1	1	0	0	1	0	0	1	0	2	1	0	0	1	1	1	0	0	2	0	0	2	1	1	1	1	1	1	1	1	1	0		
<i>U. uncia</i>	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0	1	1	2	0	0	2	0	1	0	1	1	0	1	1	0	0	0	1	0		
<i>P. atrox</i>	1	1	2	1	1	0	1	x	0	1	1	1	2	1	1	1	1	1	2	1	1	0	0	1	1	1	0	1	1	1	2	0	0	1		

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2																											
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
<i>P. lemanensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. leo</i>	1	0	1	1	1	2	1	1	0	1	0	1	0	0	1	1	1	2	1	2	1	1	1	0	1	1	1	0
<i>P. tigris</i>	1	1	1	1	1	2	2	1	0	1	0	1	1	1	1	1	0	2	0	2	0	1	1	1	2	0	1	0
<i>P. onca</i>	1	1	1	1	1	0	1	1	0	1	0	0	1	1	1	1	0	2	1	2	0	1	1	1	2	1	1	0
<i>P. pardus</i>	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0
<i>N. nebulosa</i>	1	0	1	1	1	0	1	0	0	1	0	0	2	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0
<i>U. uncia</i>	1	0	1	1	1	1	2	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	0	1	0	1	0
<i>P. atrox</i>	1	1	1	1	1	1	1	1	x	0	0	1	1	1	1	1	0	2	1	2	0	1	1	0	1	1	1	1

	1 1 1 1 1 1 1 1 1 1 2 2 2																											
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
<i>P. validus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. leo</i>	2	2	1	1	0	1	1	1	0	2	1	0	1	0	1	1	2	1	0	0	1	0						
<i>P. tigris</i>	2	2	0	1	0	1	1	0	0	0	1	0	1	1	1	1	2	0	1	1	1	0						
<i>P. onca</i>	0	1	1	1	0	0	0	1	0	0	1	0	1	1	1	1	1	0	1	1	2	0						
<i>P. pardus</i>	1	2	1	1	1	1	0	0	0	1	1	1	1	0	1	0	1	0	1	1	2	0						
<i>N. nebulosa</i>	0	1	0	0	0	1	0	0	1	1	1	0	1	1	0	0	2	0	0	1	1	0						
<i>U. uncia</i>	1	2	0	0	0	1	1	0	0	1	1	0	1	1	0	0	2	1	0	0	2	0						
<i>P. atrox</i>	1	1	0	1	x	1	1	1	0	2	1	0	1	1	2	1	1	0	1	0	2	1						

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King, Leigha M. and Steven C. Wallace. In review 2011. Sexual dimorphism in the Black Footed Ferret (*Mustela nigripes*) revealed by geometric morphometrics. Current Research in the Pleistocene.



King, Leigha M., Peg Yacobucci, and John Farver. 2010. Use of finite element analysis to determine the optimum angle of Thescelosaur (Dinosauria) metatarsals. Journal of Vert Paleo, SVP Programs and Abstracts Book, 115A.

King, Leigha and Joe T. Elkins. 2007. Gender differences and results of the Geoscience Concept Inventory on field based programs. Geological Society of America Abstracts with Programs, Vol. 39, No. 6, p. 317

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2011 Don Sunquist Center of Excellence in Paleontology \$200  
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2008 Toledo Gem and Rockhound \$450  
2008 BGSU Undergraduate Research (ASUR) \$250  
2007 MS Loughheed Book Award \$250  
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2006-2009 University Professors Scholarship \$34,296  
2006-2009 Sigma Gamma Epsilon, held position of Secretary